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JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

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Survival of Marked Lake Trout in Lake Manitou, Manitoulin Island, Ontario[1,2]

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ABSTRACT

Lake trout (491 in all), *Salvelinus namaycush*, planted as yearlings in Lake Manitou in 1952 were tagged at age VII when taken in trap nets during spawntaking operations. At the same time 259 native adult trout of unknown age were also tagged. In spawntaking operations in subsequent years tag numbers were noted for tagged fish recaptured and the fish returned to the lake after normal spawntaking. Both groups were estimated to have suffered a decrement of 25% per year. The lake trout planted were given a distinctive fin clip on planting so that comparisons of recaptures of tagged and untagged planted fish permitted estimates of the survival of the total plant. The mean annual mortality rate from the time of planting was also estimated at 25%. Trout planted later appeared to have suffered a similar mortality rate. Observations on planted lake trout of known age indicated that the peak age for first spawning in females was age VI. There is no predation by sea lamprey in Lake Manitou.

Lake Manitou (45°70′N, 82°W) has an area of approximately 40 miles^2 and lies on Manitoulin Island in northern Lake Huron. It has a lake trout population long exploited by anglers. A creel census of the lake undertaken by the Ontario Department of Lands and Forests from the South Bay Fisheries Station in the years 1947 through 1950 showed that the smaller fish characteristic of oncoming year-classes were lacking in the lake trout catch. It was concluded, therefore, that reproduction of lake trout there was suppressed, as it apparently is elsewhere (Fry, 1939) in certain fish-eating populations of lake trout. Accordingly a plant of 10,000 yearling lake trout of a mean length of 3.7 inches (49 fish/lb) was made in the lake in November 1952 to determine whether such a plant would add significantly to the fishery. The planted fish were stock from the Montreal River run of Lake Superior (Loftus, 1958) and were marked by the removal of the adipose fin. By 1957 it appeared that the fish of the 1952 plant were surviving well and a second plant of 29,000 yearlings (mean 1. 2.5 inches), similarly marked, was made in May 1958, the fish being of Lake Manitou stock. Further plants, mainly of Lake Manitou stock, bearing various marks have been made annually, those up to 1961 being indicated in Table I. Survival from all these plants appears to have been substantial but the present report deals predominantly with the 1952 plant.

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[1]Received for publication March 14, 1968.

[2]Contribution No. 68-2 of the Ontario Department of Lands and Forests, Research Branch, Maple, Ont.

[3]Deceased September 15, 1962.

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TABLE I. Sightings of planted and native fish in spawntaking operations, 1959–65.

Year of planting or tagging	Mark	Fork length (*inches*)	No. planted	No. sighted						
				1959	1960	1961	1962	1963	1965	1965
			Finclipped at planting							
1952	Adipose	3.7	10,000	800[a]	667	926	1059			
1958	Adipose	2.5	29,000					811	553	584[c]
1959	Left ventral	3.0	10,000				96	618	1015	698[c]
1960	Right ventral	2.8	14,000[b]					144	516	790
1961	Right ventral and left pectoral	–	10,000							277
			Tagged or unmarked							
1958	Tagged, native			63	43	38	15	4	5	1
1958	Tagged, planted			394	402	211	198	24	27	29
	No mark			928	732	679	662	393	964	1913

[a]After October 13 only.
[b]10,000 additional planted with no marks.
[c]Some of the 1962 plant may be confused here.

In 1958, 491 trout of the 1952 plant, taken in the nets for spawntaking, were tagged. At the same time 259 native (unmarked) lake trout were also tagged. In each subsequent year the spawntakers examined their catches for tagged and finclipped fish so that it was possible to estimate the survival of the two samples of tagged fish and also the numbers of untagged, finclipped fish present in certain years. Thus the survival of the 1952 plant was estimated with some certainty. From these quantitative estimates for that year-class, together with the numbers of sightings of fish from other plants, it was also possible to gain a general appreciation of the survival of the second plant.

The determination of the mortality of lake trout in Lake Manitou is of particular interest because that lake has been invaded by the American smelt, *Osmerus mordax*, which has become a major item in the diet of the lake trout. The smelt has been blamed by many commercial fishermen for the catastrophic loss of the lake trout from the upper Great Lakes. Although Lake Manitou has received a population of smelt, it has not been invaded by the sea lamprey, *Petromyzon marinus*, which is the other recent newcomer to the upper Great Lakes also held responsible for the loss of the lake trout. A plant of the same stock of Montreal River lake trout was also made in South Bay in 1952, an arm of Lake Huron where the lamprey is abundant. The mortality of this plant has already been reported (Budd and Fry, 1960) so that a direct comparison can now be made as to survival between these two lots of trout. An estimate of the natural mortality rate of lake trout is also available for the population of Lake Opeongo (Paloheimo, 1958; Beverton and Holt, 1957), where there are neither lamprey nor smelt.

In addition to providing information on survival, the recapture of the marked fish has given us records of the growth rate and age at maturity of the lake trout in a lake in which the assessment of the age of this species by the scale method has so far been unsatisfactory.

METHODS

Spawntaking operations in Lake Manitou were carried out with four 16-ft trap nets set for a period of 2–3 weeks in October. The cribs had web of approximately 2½-inch stretched mesh. Cotton nets were originally used but were gradually replaced by ones of synthetic fibre. The cotton leads were 6-inch mesh. The nets were set in the years covered by this report in the positions indicated in Fig. 1. Thus two nets were fished continuously in the same

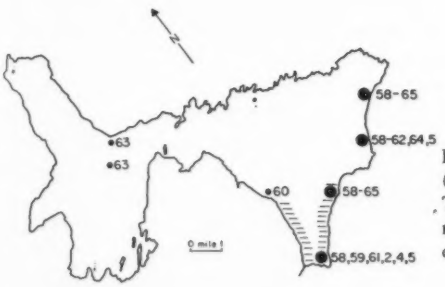

FIG. 1. Lake Manitou, showing locations (●) of four trapnets fished in various years. The hatched area of the shoreline shows the region where the 1952 plant was made. One of the traps was moved for 1960, and two for 1963.

locations throughout the period and the others were fished predominantly at constant sites. The sites where the nets were ordinarily set are in the part of the lake where the yearlings were planted in 1952.

The fish were tagged during the spawntaking operations in 1958 by two of us who accompanied the spawntaking crew. Oval celluloid streamer tags ($\frac{3}{8} \times \frac{1}{2}$ inch) with the numbers protected by transparent laminations were used. The tags were red, green, or yellow, the majority being yellow. They were fixed through the musculature just anterior to the dorsal fin by a loop of 6-lb test monofilament nylon. The nylon was fixed to the tag by a fly-tyer's knot and passed through the muscle and then back through the eye of the tag by an ordinary needle. The loop was drawn up to bring the tag close to the back of the fish and the free end of the nylon was then snugly secured by at least three half hitches about the loop adjacent to the tag. The excess filament was then trimmed to about half an inch.

The fork length of each fish was measured to the nearest half-inch when it was tagged. A record was kept of all the lake trout handled in the nets as to whether they were hard or ripe. Subsequent to 1958, all operations were carried out and records kept by the spawntaking crew, whose data were later consolidated into an annual summary by the manager of the Tarentorus Hatchery in the Sault Ste. Marie Forest District.

Tag returns by anglers were made voluntarily, but these returns in later years were facilitated by the activities of the local conservation officer, Mr A. Zimmerman, who has maintained a creel census of Lake Manitou in recent years as part of his regular duties.

The tag returns, together with the estimated numbers of the tagged fish extant in various years that were derived from them, are given in Table II. In all, 400 (82%) of the planted fish bearing tags and 111 (43%) of the native fish were recovered at least once. There were many multiple recoveries (e.g., Tables III and IV) but no complete summary of the multiple recoveries was prepared.

TABLE II. Planted and native fish tagged in 1958 and estimates of numbers of tagged fish extant, 1958–67. See text for explanation of symbols.

Year	n	m	C	R	K	$\hat{N}$
			Planted stock			
1958	491	491	327	327	–	491
1959	202	199	251	126	3	399
1960	192	190	187	128	2	280
1961	134	134	144	91	0	212
1962	121	113	65	42	8	183
1963	22	18	54	11	4	92
1964	28	24	40	14	4	73
1965	21	19	22	5	2	86
1966	14	11	11	3	3	$\geq$22
1967	11	6	0	0	5	$\geq$11
			Native stock			
1958	259	259	104	104	0	259
1959	47	44	78	21	3	166
1960	32	30	60	14	2	131
1961	30	30	35	6	0	175
1962	13	8	25	2	5	105
1963	6	4	20	1	2	82
1964	4	3	17	1	1	52
1965	3	0	14	0	3	$\geq$17
1966	13	4	3	0	7	$\geq$13
1967	3	1	0	0	2	$\geq$ 3

TABLE III. Numbers of native and planted fish tagged in 1958 that were seen at various intervals in trapnets set for spawntaking. Multiple sightings in a given season were considered as a single event. $\chi^2 = 37$, $P < 0.005$. Sightings to end of 1965.

	No. released	Interval, *years*				
		1	2	3	4	5+
Native	259	73	27	17	9	10
Planted	491	417	153	29	18	8

TABLE IV. Recoveries, after year of tagging, of planted fish seen again and of those not seen again in year of tagging. $\chi^2 = 0.22$.

	No. released	No. recaptured after 1958
Seen again in 1958	256	164
Not seen again in 1958	235	161

There were proportionately far fewer native fish recovered than planted ones, as is indicated by the percentage recoveries given above. The difference in the rates of recovery of the two series of tags appears to lie in a difference in the behaviour of the two lots of fish rather than in mortality rates.

At first it was thought that handling the fish for spawntaking might have brought about extra mortality in the native fish since these were predominantly mature fish. However, an at least partial test showed that such was not likely the case. It is common practice for spawntakers to hold in their nets mature fish which are not ripe when first captured. Such fish may be handled several times in successive lifts before they are ripe and their spawn is taken. Records in 1958 were kept of fish tagged and so held. Of 85 fish that were retained, 65% were seen again in subsequent years whereas, of 185 fish spawned without holding, 69% were seen subsequently. There is no significant difference between these two fractions.

As the years passed it became apparent that, although the planted fish bearing tags were being seen again each year in large numbers, many of the native fish that were recaptured had not been seen since their initial release. A quantitative expression of this phenomenon (Table III) suggests that the native fish did not regularly return each year to the vicinity of the spawntaking nets and so were not recaptured as frequently as the planted fish.

POPULATION ESTIMATES

When a tagged population is fished in consecutive years and the captured individuals are returned to the water, an estimate of the tags extant in a given year can be made from the recaptures in the subsequent years, as was pointed out by H. A. Regier, University of Toronto, who was kind enough to do some preliminary analysis of the data and to provide the method adopted here.

The estimator used was the maximum likelihood estimator devised by D. S. Robson (personal communication)[4] for a multiple mark–recapture experiment using the hypergeometric probability distribution as the sampling model. This method has not yet been published but is an extension of the ideas expressed in Robson and Regier (1968).

[4]See also Robson, D. S. Unpublished. Mark-recapture methods of population estimation. Paper BU-168 in the Biometrics Unit, Cornell University. 32 p.

The estimator is:

$$\hat{N}_i = n_i + m_i (C_i - R_i)/R_i$$

where $\hat{N}_i$ = estimate of population at the time the ith sample is taken; n_i = the number captured in the ith sample; m_i = the number returned to the population from the ith sample. (In the present case, the tagged fish handled in a given spawntaking operation less those killed by angling in the same year — column K_i in Table IV); C_i = the number of tagged fish captured after the ith sample whether handled in year i or not (i.e. the virtual tagged population of year $i + 1$); and R_i = the number out of m_i which were later recaptured.

The fish captured in a given year are taken collectively as the ith sample.

Table IV shows statistics used for a chi-square test of the hypothesis that no fish died immediately after tagging; the chi-square obtained was 0.22 showing no cause to reject the hypothesis.

With estimates of the numbers of planted fish bearing tags extant in various years it is then possible to make estimates (Table V) of the total numbers of planted fish vulnerable to the nets, since records were kept of the sightings of both tagged and marked fish (Table I).

TABLE V. Estimates of numbers of fish planted in 1952 and 1958[a] that were vulnerable to trapnets during spawning runs, 1959–63.

Year trapped	Age	Clip sightings	Tag sightings[b]	Estimated tags extant	Estimated no. vulnerable to nets
1959	VIII	800	394	395	1200
1960	IX	667	402	276	730
1961	IV+X	926	211	206	1100
1962	V+XI	1138	198	176	1200
1963	VI+XII	811	24	94[c]	3300

[a]Marked by removal of adipose fin in both years.
[b]Out of 491 fish planted in 1952 and tagged in 1958.
[c]Extrapolated.

Since a certain number of tags were incorrectly read, and thus these sightings could not be assigned to either the planted or the native lots, the sightings referred to planted fish are slight undercounts. However, in the years 1959–62 there were only 36 such unplaced sightings. If all these were assigned to planted fish the estimates given in Table V would be reduced by approximately 3%. It is not felt that such a correction is worth introducing.

Firm estimates of the numbers of planted fish could be made only for the years 1959–62, since these were the only years in which substantial numbers

of tagged fish were sighted, but an estimate was also made for 1963 because a substantial proportion of the fish of the 1958 plant could have been expected to be first mature in that year (age VI).

MORTALITY RATES OF ADULT LAKE TROUT

The estimates for the numbers of tagged planted fish extant in various years (Table II, Fig. 2) show a regular decrease in the population at a rate

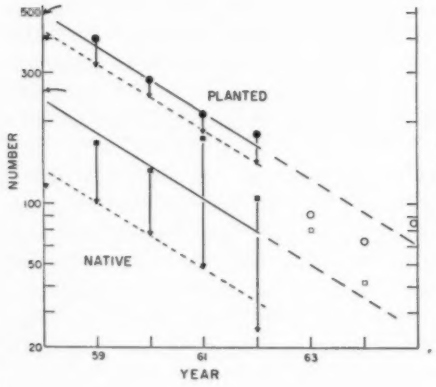

FIG. 2. Survival of fish tagged in 1958. Circles, Robson estimates for planted fish; squares, for native fish. Triangles, minimum populations. Lines fitted by eye to origins (arrows) and solid points. Data from Table II.

of 25% per year as indicated by the slope of the solid line drawn through the data. The population estimates for the native trout tagged, which are much less reliable, show a much greater scatter of points. No independent estimate was made of the mortality rate of the native fish, but it is considered that the mortality rate for them was the same as that for the planted ones. The solid line drawn through the points for the native fish was simply drawn parallel to the one through the estimates for the planted fish.

The triangles given below the points for the population estimates in Fig. 2 over the years 1958–62 represent the numbers of tags known to be extant in the various years because they were sighted in those years or subsequent ones, i.e. the virtual populations (Fry, 1949). Thus these data give a floor to the population estimates and can be taken as the lower limits of the various population estimates in lieu of statistical computations. Moreover, if fishing effort is constant and observations are continued until the total extinction of the group concerned, the slope of the line joining the successive counts of the virtual population will represent the annual mortality rate. From 1959 to 1962 fishing effort on the tagged population was essentially constant and the points for those years for the planted fish fall on a straight line parallel to the line drawn through the population estimates. The point for 1958 falls a little below the line, as would be expected since all fish were not tagged at the beginning of the fishery. The virtual populations for the

native fish again show a wider scatter than the data for the planted fish but the slope is of the same order.

The distances of the virtual population points from those of the Robson estimates for the two lots of tagged fish give a still further indication that the lot of native fish tagged were not as vulnerable to the fishery as were the planted lot. The closer the proximity of these two estimates for the same population the more intensive has been the fishery on which they are based.

The mortality rates represented by the decline of the estimates of the numbers of fish bearing tags include natural and fishing mortality, tag loss, and indeed some emigration. Four planted fish bearing tags were reported in 1959 from waters other than Lake Manitou. Three of these were taken in Providence Bay, Lake Huron, not far from the mouth of the Manitou River which drains Lake Manitou. The fourth was taken in the northwest corner of Georgian Bay. However, it is presumed that emigration caused a negligible drain on the population.

Tag loss can probably also be taken as negligible. As Table IV shows, there was little immediate post-tagging loss. No tests for continuing tag loss were made in Lake Manitou by combining finclipping with tagging, but such tests in South Bay with trout tagged by the same workers indicate tag loss to be negligible over the first 2 or 3 years after release, and it is conservative to consider tag loss negligible in Lake Manitou also. Observations over longer periods in South Bay were prevented by heavy predation of the lake trout by the sea lamprey.

Fishing mortality of the tagged fish must also be considered to be low, since up to the end of June 1966 the total return of tags by anglers was only 47, 20 from native and 27 from planted fish. An additional 2 native and 3 planted fish with tags were taken by anglers in 1967. However, 40 of the returns to 1966 were received after 1961, so that it seems likely that, at least in the earlier years, the returns were by no means complete, and it is, of course, largely for these earlier years that the estimate of mortality was made. Since 1961 the minimum estimate for deaths by annual fishing is 2% per annum, which is still almost negligible. The evidence available suggests that the annual loss of 25% seen in the tagged, planted population must be largely assigned to natural mortality and that the natural mortality rate of the Lake Manitou trout is therefore of the order of 20% per year. Paloheimo (1958) estimated the natural mortality rate of the Lake Opeongo lake trout age IX and older, a population which is not associated with either the lamprey or the smelt, to be of the same order, 16%. Thus in Lake Manitou at least, the smelt does not appear to influence adult mortality of the lake trout.

SURVIVAL OF PLANTED LAKE TROUT

The five lower right-hand circles shown in Fig. 3 represent the estimates for the total population of planted fish vulnerable to the trap nets in the respective years given in Table V. These fish are the survivors of the plants of 1952 and 1958. Since the two lots bore the same mark, ablation of the adipose

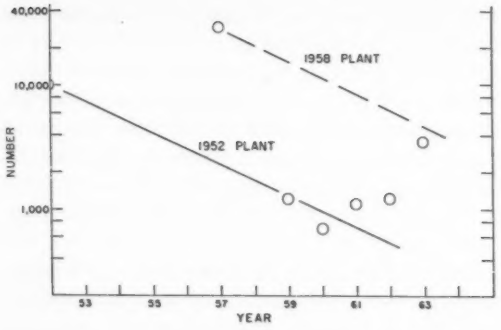

FIG. 3. Estimates of the survival of the lake trout plants of 1952 and 1958. For explanation see text.

fin, and since neither size nor age was regularly recorded for the fish handled, it was not possible to precisely determine the proportions of the two groups in the catches.

It is certain that none of the 1958 plant were among the planted fish taken in 1959 and highly improbable that any substantial number of them were taken until 1961. In that year 6 out of 11 fish examined from the traps were age IV, so that, although no quantitative significance can be attached to such a small sample, there was probably a substantial entry of the 1958 plant into the catch made during the spawning run of 1961. Of the fish handled in 1961 that had the adipose fin clipped, 70% were males in contrast to 45% for the 1960 catch. If the change in sex ratio can be ascribed to the influx of a new group consisting of males only, then the 1958 plant would have made up one third of the 1961 spawning run of planted fish. Such an estimate is a minimum one since there may have been some 4-year-old females in the run, but that is not likely. In addition there was a drop in the fraction of males in the tagged members of the 1952 plant from 54% in 1959 to 41% in 1962 which, if it were a reflection of the change in the sex ratio of the total planted population, might indicate a greater influx of new males than the minimum estimate above. In 1963 it can be expected that the 1958 plant would have predominated in the catch of fish with the adipose fin clipped.

The population estimate for the planted fish in 1960 falls below that of 1959 by about the same proportion as the respective difference found in the estimates for the tagged fish. Moreover, a similar rate of decrease, at least as a mean rate, appears to have taken place throughout all the preceding years after the planting. The original plant is indicated by a semicircle in the upper left corner of Fig. 3. The line drawn down from the point indicating the plant towards the population estimates for 1959 and 1960, which are taken to indicate its survivors, was drawn to represent an annual mortality rate of 25%, the rate found for the tagged fish of the 1952 planting for the years 1959–61. The line thus drawn falls slightly above the estimates for the finclipped fish in 1959 and 1960. It is reasonable that it should do so since a certain proportion of planted fish may not bear recognisable finclips. In the

case of the 1952 plant in Lake Manitou there is an estimate of such error, since some of the same lot were planted in South Bay, where there were no native lake trout at the time. Of 236 fish of this plant examined from South Bay, 14% did not have a recognisable adipose clip. Taking into account a similar unmarked fraction in the plant in Lake Manitou, the line as drawn comes very close to an estimate of the planted population that includes the unmarked fraction and suggests that the mortality rate as measured for the tagged fish after 1958 held also for the planted population during the early years after planting.

A less acceptable estimate can be made of the survival of the 1958 plant. The first year for which any possible estimate of the number of survivors of that plant can be made is 1963. The estimate of the number of tagged fish extant in that year has to be by extrapolation. A further weakness of the 1963 data is the paucity of sightings of tagged fish. With these weaknesses in mind it can be seen that not too much reliance can be placed on the estimate of 3300 given in Table V. However, that estimate represents a mortality rate of the same order as the one suffered by the 1952 plant, as the broken line in Fig. 3 indicates. Since the 1958 plant was made in the spring, the planting date was plotted as 1957 rather than 1958, so that the mortality rate of the plant may have been somewhat greater than the figure suggests, but not unduly so.

Estimates of the success of the various other plantings can only be general assessments based on data which are given in Table I. Fish of the various plants appeared regularly in the catches and were sighted in essentially comparable numbers when at given ages, indicating similar rates of survival.

GROWTH AND MATURITY

Samples from three plantings of the lake trout were taken at various ages and measured (Fig. 4), the plantings being recognised by their distinctive fin clips. The three plants all appear to have grown at a similar rate, which

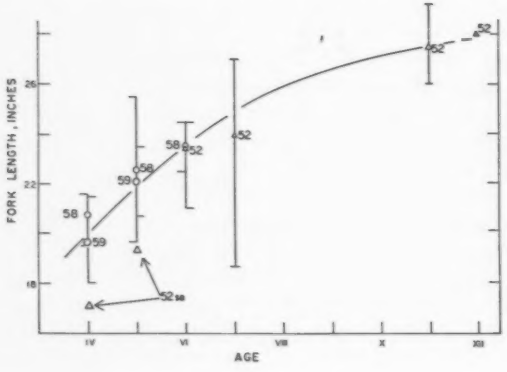

FIG. 4. Growth of lake trout planted in Lake Manitou as determined from recaptures from three plantings of finclipped fish. The bars show the ranges found in the various lots. For comparison, the sizes attained at ages IV and V in South Bay, Lake Huron, of two samples of the same stock as the 1952 plant (Fry and Budd, 1958) are shown.

presumably depends on the conditions in Lake Manitou. The fish attained a length of 20 inches in their 5th year. Two points showing the sizes attained at ages IV and V by the lot of the 1952 plant that were released in South Bay suggest that growth in South Bay was not as rapid as in Lake Manitou, but by age V in South Bay the lamprey have already selectively removed most of the larger trout. Further, the mean sizes for South Bay are based on samples taken throughout the summer whereas the Lake Manitou samples were taken in October only.

On the basis of age assessment by scale reading, lake trout females are generally considered to be largely mature by age VII. Observations of the age at first maturity were available for the planted stocks in Lake Manitou from the spawntakers' records. As each female was spawned, it was examined for fin clips. Thus the first substantial appearance of females of a given plant in the spawning records can be taken as indicating the age at first maturity.

Females of the 1952 plant were mature in 1958 (i.e. age VII), when observations were begun. This plant did not, however, contribute to the spawn collection since these fish did not ripen in synchrony with the Lake Manitou stock. In the years 1958–60 the females of the 1952 plant were still hard at the end of the spawntaking operations. In 1961 they were spent before netting began. The later plants, which were of Lake Manitou stock, contributed substantially to the spawn collected. The 1958 and 1959 plants made their highest contributions of eggs at age VI. The 1960 plant contributed substantially at age VI but it remains to be seen whether this was the peak contribution. A few females of the 1961 plant were mature at age V, as were a few in the earlier plants. A major contribution was made by fish with clipped adipose fins in 1962, when the 1958 plant was age V, but it is possible that some of this contribution was made by surviving members of the 1952 plant. The direct evidence of age at first maturity of female lake trout in Lake Manitou indicates a substantial fraction of the females to be mature at age VI, as elsewhere.

ACKNOWLEDGMENTS

Mr K. M. Hazzard, Hatchery Assistant, assisted in operations in 1958. Mr A. H. Draves, Fish Culturist, was responsible for the records gathered from 1959 to 1964 inclusive. Mr G. A. Clark collected the records in 1965. The trapnets were operated first by Mr R. G. Brigden who was followed in turn by Mr A. R. Humphreys and Mr E. Macaulay.

We are once more most indebted to Mrs G. W. Bennett of the South Bay Fisheries Station for the excellence of the records available there.

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Bryozoa (Polyzoa) of Arctic Canada[1]

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ABSTRACT

Ninety-three species of Bryozoa are reported here from the area of arctic Canada extending from Belle Isle Strait westward to Herschel Island. Bathymetric and distributional data, both local and regional, are given for all species. Photomicrographs are provided for 47 species. One species, *Stomachetosella hincksi*, is described as new. *Electra crustulenta* (Pallas) var. *arctica* Borg is accorded specific rank. *Callopora smitti* Kluge is referred to the genus *Copidozoum* and *Hippodiplosia obesa* (Waters) is transferred to the genus *Schizoporella*. A new family, Hincksiporidae, monotypical for *H. spinulifera* (Hincks), is attributed to the Ascophora Imperfecta. *Porella princeps* (Norman, 1903b) is considered to be a synonym of *Pachyegis producta* (Packard, 1863), and *Codonellina operculata* Mawatari (1956) a synonym of *Schizomavella porifera* (Smitt, 1867). The following eight species are new for arctic Canada: *Terminoflustra barleei*, *Scrupocellaria arctica*, *Reginella spitzbergensis*, *Hippoporina cancellata*, *Schismopora nodulosa*, *Escharella thompsoni*, *Smittina mucronata*, *Pseudoflustra sinuosa*. Except for *R. spitzbergensis* and *H. cancellata*, these are also new for arctic North America.

The zoogeographical relationships of the fauna are discussed, three main types of distribution being recognised, viz., panarctic, boreal-panarctic, and Atlantic–arctic. No relationship between faunal distribution and the surface waters of the arctic and subarctic zones is apparent, the majority of species transgressing both. Compared with the bryozoan fauna of the antarctic region, the arctic group is impoverished in indigenous taxa.

INTRODUCTION

This report is primarily based on the results of a detailed examination of the collections of Bryozoa taken by the M.V. *Calanus* in the waters of the eastern and central Canadian arctic and subarctic between 1947 and 1965 and the M.V. *Salvelinus* in the western Canadian arctic between 1960 and 1965. The total area represented by these sublittoral collections extends from Belle Isle Strait in the northwest Atlantic, westward to Herschel Island in the Beaufort Sea (Table I).

The opportunity was also taken to include previously unreported material from collections in the National Museum of Natural Sciences (N.M.C.), which were taken from the following localities: Lake Harbour, Baffin Island, N.W.T.; Mould Bay, Prince Patrick Island, N.W.T.; Isachsen, Ellef Ringnes Island, N.W.T.; also some small collections off Newfoundland which were obtained during the 1963 cruise of the *A. T. Cameron*.[2] This material is designated in the text by National Museums of Canada catalogue numbers; Fig. 1 shows the geographical locations of stations and catalogue numbers.

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[1]Received for publication May 23, 1968.

[2]All of the above mentioned vessels are owned and operated by the Fisheries Research Board of Canada.

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TABLE I. *Calanus* and *Salvelinus* collection stations, 1947–65.

Station	Collection No.	Date	N lat	W long	Depth (*m*)	Bottom
7	B-3	3 VII 47	58°55′	68°53′	10	Rock
11	B-4	12 VII 47	59°11′	68°47′	46	Rock, sand
13	P-19	13 VII 47	59°30′	69°00′	39	–
20, 21	B-6	18 VII 47	59°53–54′	69°29–31′	64	Rock, sand, mud
28	B-11	18 VII 47	58°54.5′	68°59′	27	Rock
30	B-12	20 VII 47	58°42.5′	68°10′	36	–
33	B-14, 15	8 VIII 48	59°13′	65°45′	18–27	Rock, mud
49	B-19	25 VIII 47	59°29′	65°26′	Shore	–
53	B-3	10 VII 48	58°38′	68°13′	9	–
58	B-3	28 VII 48	60°05′	65°06′	20	–
102	B-2	30 VI 49	60°23.5′	64°52′	90–130	Rock, mud
103	B-3	7 VIII 49	60°24′	64°58′	145–275	Rock
106	B-5	7 VIII 49	60°21′	64°58′	100–110	–
107	B-6	7 VIII 49	60°22′	64°47′	55–73	–
126	B-11	23 VIII 49	60°22′	69°26′	70–91	Rock
201C	B-1	29 VI 50	59°29.5′	65°20.5′	80–100	Mud
203	B-2	8 VII 50	58°50′	68°18′	30	–
206	B-3	15 VII 50	60°45′	69°17′	90	–
208	B-4	20 VII 50	61°05.3′	69°34′	82	Rock
210	B-5	21 VII 50	61°04.5′	69°39′	90–110	Rock
212	B-14	21 VII 50	61°02′	69°38′	Shore	–
221	B-14	4 VIII 50	62°12′	69°38′	274	–
225	B-11	12 VIII 50	60°40.5′	64°39.7′	22	Rock
226	B-12	13 VIII 50	60°38′	64°38.9′	90–100	–
229	B-14	26 VIII 50	59°29′	65°17.5′	13	–
231	B-13	27 VIII 50	59°28.5′	65°15′	63–90	Rock, mud
232	B-14	27 VIII 50	59°23′	65°01′	10	–
317	B-2	9 VIII 51	62°44′	65°29′	26–36	Rock
318	B-2	9 VIII 51	62°43′	65°38′	55	–
319	B-6	11 VIII 51	62°21′	65°16′	113–118	Rock
321	B-7	11 VIII 51	62°23′	64°58′	71	–
322	B-9	12 VIII 51	62°46′	65°55′	119	Sand, gravel
331	B-11	22 VIII 51	62°42′	65°31′	77	–
333	B-12	24 VIII 51	62°39′	65°47.5′	137	–
334	B-13	24 VIII 51	62°38′	65°52′	183–192	–
406	B-3	22 VII 52	62°74′	65°26.5′	46	–
413	L-2	5 VIII 52	66°12.5′	66°24′	Shore	–
612	B-17	8 IX 53	63°27′	84°08′	21	Rock
520	B-5	4 VIII 53	62°27′	79°51′	73–137	Rock
542	B-13	28 VIII 53	62°24′	77°56′	38	–
547	B-15	3 IX 53	63°41′	80°12′	73	Rock
549	B-16	3 IX 53	63°36′	82°00′	73–75	"
553	B-19	13 IX 53	63°09′	92°25′	36–73	"
608	B-3	9 VIII 54	62°44.5′	83°39′	32	"
609	B-4	10 VIII 54	62°57.5′	82°43′	18	"

(*Continued*)

TABLE I. *Calanus* and *Salvelinus* collection stations, 1947–65.

Station	Collection No.	Date	N lat	W long	Depth (*m*)	Bottom
610	B-5	10 VIII 54	62°58.5′	82°41′	36	Sand, mud, rock
611	B-6	10 VIII 54	62°59.7′	82°39′	49	Rock, clay
613	B-9	12 VIII 54	62°57.2′	81°50′	198	Rock
614	B-14	12 VIII 54	62°56′	81°53′	17–18	Sand
616	B-16	16 VIII 54	63°15.5′	83°41′	85–90	Rock
625	LD-4	26 VI 54	64°20′	75°34.5′	Shore	–
704	B-4	23 VII 55	56°43′	61°38′	0–22	Mud
707	B-9	12 VIII 55	62°11′	79°12′	36	–
715	B-14	19 IX 55	69°34′	80°17′	0–15	Sand, mud
719	B-22	29 IX 55	69°20.5′	81°43.5′	52	Mud
722	B-19	29 IX 55	69°20′	82°00′	36–45	"
723	B-4	4 IX 56	69°22.7′	81°44.3′	20–22	"
805	B-20	5 VIII 56	68°46′	81°11′	9	Rock
808	B-25	15 VIII 56	70°08.4′	82°20′	160–174	Mud
811	B-27	17 VIII 56	69°37.2′	81°06.3′	106	Rock
815	B-29	18 VIII 56	69°43.2′	82°07′	55	–
818	B-32	26 VIII 56	69°24′	80°53′	55	Rock, mud
820	B-34	28 VIII 56	69°55.7′	80°19′	73	Mud
821	B-37	29 VIII 59	70°00.5	80°12′	13–30	Mud
828	B-43	7 IX 56	69°25.7′	78°33′	27	Rock
837	B-45	8 IX 56	69°16′	77°48′	45–55	Sand, rock
901	B-56	29 VIII 57	69°06′	79°11′	0–34	Mud, sand, rock
58-3	B-2	24 VI 58	56°25.5′	78°55.5′	6–7	Rock
58-21	B-14	6 IX 58	62°36′	78°16′	50–53	Rock
58-28	B-19	10 IX 58	59°04′	80°27′	115	Mud, rock
58-33	B-23	8 IX 58	57°23′	79°39′	90–95	Mud, rock
59-2	B-3	21 VI 59	52°00′	80°00′	23	Rock
59-6	B-5	3 VI 59	52°55′	79°58′	65	Mud, sand, rock
59-21	B-16	21 VII 59	56°28′	78°04′	50	–
59-29	B-22	3 VIII 59	55°50′	80°15′	40	Rock
59-38	B-28	9 VIII 59	56°09′	76°26′	95–130	Mud
59-40	B-29	10 VIII 59	56°18′	76°17′	42–46	Mud
59-46	B-34	17 VIII 59	58°24′	78°19′	100	Rock, mud
59-50	B-36	16 VIII 59	58°00′	79°38′	50–60	Rock
59-58	B-44	26 VIII 59	54°24′	80°08′	62–70	Mud, rock
59-66	B-49	31 VIII 59	55°45′	82°24′	70	Mud
59-68	B-50	31 VIII 59	59°16′	82°16′	100–107	Mud
59-69	B-51	31 VIII 59	56°16′	82°42′	126	Mud, sand, gravel
60-1001		26 VII 61	69°32.5′	138°55′	13–35	Mud
60-1008		1 VIII 60	69°33.8′	138°55′	5–11 "	"
60-1035		25 VIII 60	69°32′	138°57′	22–44	"

(*Continued*)

TABLE I. *Calanus* and *Salvelinus* collection stations, 1947–65.—(*Concluded*)

Station	Collection No.	Date	N lat	W long	Depth (*m*)	Bottom
61-1	B-1	21 VII 61	60°24′	93°55′	60	Rock, mud
61-2	B-2	22 VII 61	61°00′	93°49′	45	Rock
61-3	B-3	23 VII 61	61°05′	93°54′	60	"
61-5	B-5	25 VII 61	62°30′	91°05′	70	"
61-8	B-7	27 VII 61	63°04′	90°24′	48–50	"
61-10	B-8	30 VII 61	63°43′	91°43′	80	"
61-11	P-31	30 VII 61	63°39′	91°27′	20–70	"
61-12	B-11	31 VII 61	63°33′	91°02′	90–100	"
61-13	B-13	31 VII 61	63°21′	90°37′	95–100	"
61-18	B-16	6 VIII 61	63°34′	87°20′	5	–
61-24	B-20	9 VIII 61	65°07′	86°45′	44–46	Rock
61-26	B-21	10 VIII 61	65°24′	86°44′	75	"
61-30	B-23	11 VIII 61	65°59′	85°45′	57	"
61-32	B-24	14 VIII 61	66°11′	84°12′	145	Mud, rock
61-34	B-24	14 VIII 61	66°28′	86°16′	145	Rock, sand, mud
61-35	B-25	23 VIII 61	65°36′	83°45′	95–125	–
61-39	B-27	25 VIII 61	65°32′	84°52′	42	Mud, rock
61-40	B-28	26 VIII 61	65°25′	84°49′	40	Rock
61-43	B-29	28 VIII 61	66°13′	85°09′	85–92	–
61-1015		10 VII 61	70°11′	128°35′	11	Mud, sand
62-001	B-15	14 VII 62	69°49.3′	130°19′	2–12	Sand, mud
62-009	B-27	25 VII 62	69°48′	130°13′	9	Hard sand
62-032		12 VIII 62	69°48′	130°19′	10	Mud, sand
62-033		12 VIII 62	69°45.8′	129°08′	16	Mud
62-049		29 VIII 62	70°07′	124°39′	14	Rock
62-2002	B-34	4 VIII62	72°45′	94°04′	40	Mud, clay
62-2003	B-23	23 VIII 62	72°45.5′	94°07′	34	Gravel
62-2012	B-27	25 VII 62	72°44.6′	94°05′	36	Mud, clay
62-2014	B-30	25 VII 62	72°44.1′	94°06′	35	Clay
62-2031	B-44	11 VIII 62	72°46.5′	94°13′	40	Mud, clay
62-2032	B-45	11 VIII 62	72°46.5′	94°15.5′	59–62	Mud, clay
62-4304	B-22	16 VII 62	76°37.3′	96°27.8′	25–50	–
62-4305	B-22	16 VII 62	76°37′	96°27.4′	40	–
63-019		12 VIII 63	69°49.7′	123°05.5′	83	Mud
65-1044		23 VIII 65	68°18.2′	109°15′	120	–
65-1048		30 VIII 65	69°09.8′	106°37′	60	–
65-1502	B-1	30 VII 65	51°26′	56°50′	Shore	–
65-505	B-4	31 VIII 65	51°20′	56°46′	55–64	–
65-1506	B-3	31 VII 65	51°49′	56°06′	99	–
65-1510	B-4	3 VIII 65	42°08′	55°38′	55–64	–

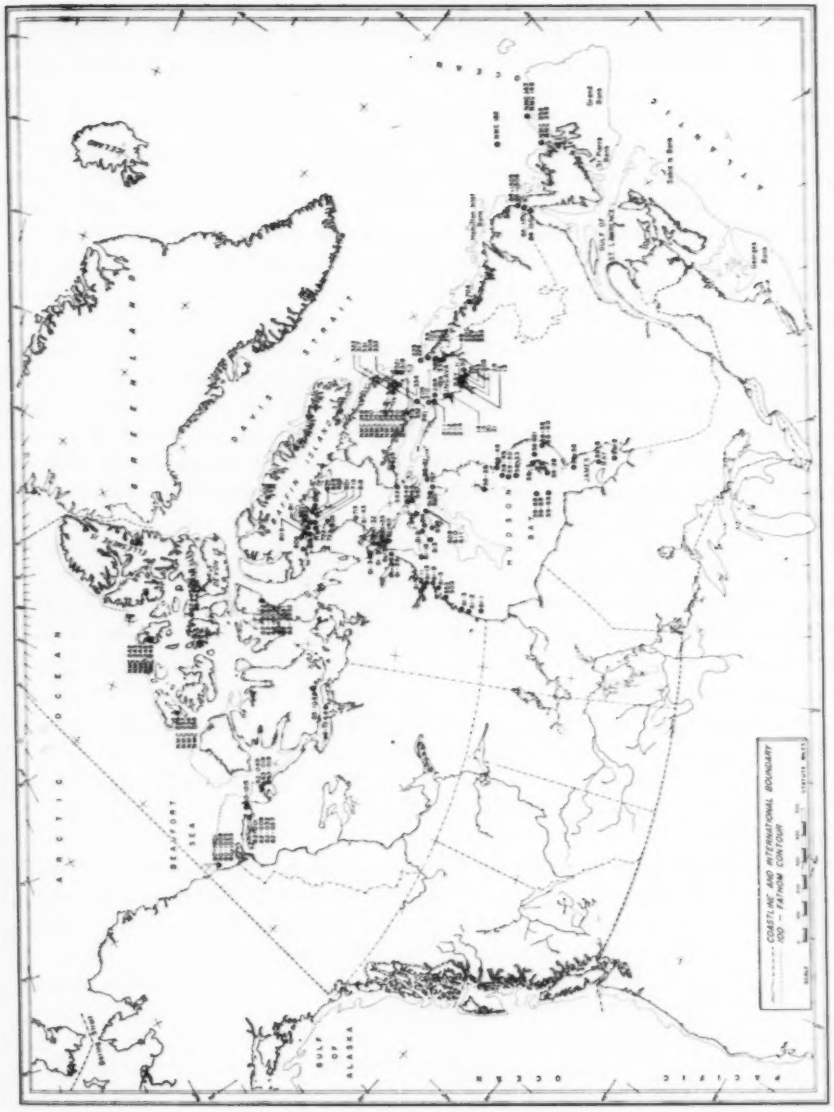

FIG. 1. Geographical locations (FRB 1947–65) and catalogue numbers (N.M.C.) cited in the text.

PREVIOUS WORK

The pertinent literature on the Canadian arctic bryozoan fauna dates from 1878[3] when Busk reported on 13 species collected from the northeastern area of the Canadian Archipelago by the North Polar Expedition (1875–76).

[3]Modified and republished in 1880.

A particularly notable contribution was made by Nordgaard (1906) in his carefully illustrated monograph of the bryozoan fauna (77 species) taken from Smith and Jones Sounds in the north and northwestern areas of Baffin Bay by the second Norwegian arctic Expedition (1898–1902). Further studies on the fauna of arctic Canada were made by Osburn (1923) who recorded 43 species collected between 115° and 165° long by the Canadian arctic Expedition (1913–18), and nine species from the *Diana* (1897) and *Neptune* (1903–04) Expeditions to Hudson Bay and Strait. Osburn (1932) reported 75 species and varieties from various collections amassed between 1897 and 1930 from Hudson Bay and Strait, and in 1936, he listed 32 species from various collections made by Captain R. A. Bartlett in northwest Baffin Bay and the central Canadian arctic. Hutchins (1940) recorded 6 species from Victoria Island, N.W.T.; Hansen (1962) incorporated material (40 species) dredged from the Canadian sector of Baffin Bay and coastal Labrador by the Godthaab Expedition (1928) in the report of the Bryozoa obtained by the expedition from West Greenland; Kluge (1962) cited several records pertaining to the eastern Canadian area, especially Labrador and Gulf of St. Lawrence which were presumably based on material that he had obtained.

The bryozoan fauna of the eastern Canadian subarctic, particularly Labrador, Newfoundland, and the Gulf of St. Lawrence is known principally from the work of Dawson (1859), Packard (1863), Hincks (1877a, 1888, 1889, 1892), Whiteaves (1901), Jullien and Calvet (1903), and Osburn (1912).

General Arrangement

The references cited for species discussed in this report usually pertain to the Canadian arctic and subarctic areas only.

Descriptive commentary of species is generally omitted as comprehensive modern descriptions are to be found either in Osburn (1950, 1952, 1953) or Kluge (1962).

Morphological terms employed throughout the text are defined by Bassler (1953). Data pertaining to species' distribution outside the North American area were drawn from several sources, but principally from Borg (1933), Mawatari (1956), Kluge (1961, 1962), and Hansen (1962).

All of the illustrated material, including the holotype of *Stomachetosella hincksi* n.sp. is deposited in the National Museum of Natural Sciences, Ottawa, Ont.

The following abbreviations appear in the text: F.R.B. — Fisheries Research Board of Canada; N.M.C. — National Museums of Canada (Museum of Natural Sciences); M.C.Z. — Museum of Comparative Zoology (Cambridge, Massachusetts); N.W.T. — Northwest Territories.

Terminology

Usage here of the terms "arctic" and "subarctic" follow that of Dunbar (1953) for the marine zones of the arctic region.

GENERAL DISCUSSION

Analysis of the distributions of the 93 species dealt with in this report reveals three principal patterns of occurrence:

(*a*) 42 species are predominately circumpolar and cold-stenothermal, terminating their southern ranges for the most part in the waters of the subarctic zone. These conform to Ekman's (1953, p. 176) panarctic type of distribution;

(*b*) 38 species have eurythermal tolerances being widely distributed throughout the boreal-panarctic regions;

(*c*) 11 species (i.e. *Terminoflustra barleei*, *Copidozoum smitti*, *Notoplites smitti*, *Kinetoskias arborescens*, *Schismopora nodulosa*, *Escharella abyssicola*, *Cystisella elegantula*, *Porella aperta*, *Porella struma*, *Pseudoflustra solida*, and *Pseudoflustra sinuosa*) with eurythermal or cold-stenothermal tolerances are confined within the area limited by the western Canadian Archipelago (125°W long) and the eastern Siberian Sea (170°E long), thereby approximating the Atlantic–arctic type of distribution of Ekman (1953, p. 180). This component (excluding *T. barleei*, *E. abyssicola*, and *P. struma*), comprises the exception to the rule "that practically all of the true Arctic species are circumpolar in distribution" (Osburn, 1923, p. 4D).

Two further patterns of distribution are exhibited by the following: *Escharella connectens* is restricted mainly to the arctic zone (high arctic in the sense of Ekman (1953)), with southern occurrences at Hudson Strait and Ungava Bay, coinciding perhaps with the intrusion of warmer Atlantic water into this area (Dunbar, 1958).

Membraniporella crassicosta is known only from Point Barrow and the northwest Atlantic (Fig. 4), despite fairly widespread collecting in the central Canadian and Eurasian arctic areas. This pattern of distribution conforms to the discontinuous circumpolar type of Ekman (1953, p. 180). The species may be a relict, equivalent to the distinctive group of miscellaneous amphiboreal invertebrates which according to Nesis (1962, p. 93) dispersed westwards from the North Pacific into the western Atlantic by way of the Canadian Archipelago, during upper Pliocene times.

To summarize: as with polychaetous annelids (Grainger, 1954) the bryozoan fauna of arctic Canada exhibits a remarkably widespread distribution throughout the arctic region, the absence of a significant high-arctic element emphasizing the marked tolerance by nearly all species to a varied range of temperature and salinity conditions. A relationship, therefore, between bryozoan distribution and the position of the arctic and subarctic zones of surface waters within the Canadian sector (see Grainger, 1966, fig. 63) is not well shown, most of the species transgressing both.

Southward from the arctic ocean, the extensive southern continuity of coastal North America, in conjunction with low summer water temperatures in the North Pacific and the cold, southward-flowing Labrador current in the northwest Atlantic, has permitted many cold-stenothermal species to achieve

a broad latitudinal distribution, mixing with boreal components at the periphery of their southern ranges, i.e. the subarctic transitional zone of Ekman (1953, p. 101).

Although Cape Cod, Massachusetts, is recognized as constituting the southern boundary for the panarctic bryozoan fauna on the North American east coast, many species are extinguished further northward (see Table II). In some instances, however, collecting data are still incomplete; for example, the following panarctic species ostensibly terminate their southern ranges in the area of Hudson Strait and the Labrador coast, yet in the western Pacific occur either in the coastal waters of the southern Kurile Islands, or the Sea of Japan: *H. nigrans*, *B. spitzbergensis*, *S. mucronata*, *R. hincksi*, and *S. obesa*.

The greatest reduction in the cold-stenothermal fauna takes place in the Gulf of St. Lawrence, panarctic species being almost entirely absent in the summer-warm surface waters of the southwestern area. Of the remaining species which persist further southwards, about half find their southern limit in the northern part of the Gulf of Maine, as a result of rapidly increasing temperatures brought about by the recyclement and warming of water within the Gulf (Schopf, 1965); the rest extend southward to Cape Cod.

The southward decline of the cold-stenothermal bryozoan fauna is less obvious on the North American Pacific coast as a result of a greater uniformity in seasonal water temperatures. Although the Aleutian Islands constitute an important southern boundary for the subarctic fauna (Osburn, 1950, 1955) the ranges of many cold-stenothermal species extend as far south as Vancouver Island and Puget Sound (Osburn, 1950), including five species discussed here, namely, *Microporina articulata*, *Stomachetosella limbata*, *Rhamphostomella costata*, *Cheilopora sincera*, and *Myriapora subgracila*.

The extent to which the rich Pacific-boreal assemblage has dispersed northward into the subarctic zone has been a subject for some conjecture, dating from Nordgaard's (1918, p. 5) hypothesis that the north polar bryozoan fauna comprises two regional components, Atlantic–arctic and Pacific. Osburn's (1950, 1952, 1953, 1955) studies of the bryozoan fauna of Point Barrow, Alaska, however, clearly demonstrated the absence of any conspicuous Pacific component within the western North American subarctic. Of the 113 species in the Barrow collection, 102 were already known from the Atlantic–arctic region (Osburn, 1955, p. 30), the remainder being new species having localized distributions. Osburn's (1955, p. 30) conclusion was therefore unequivocal: "there is no significant difference between the bryozoan faunas of the Pacific-Arctic and Atlantic-Arctic areas."

Hansen (1962, p. 62) suggested that a small assemblage (10 species) of circumpolar bryozoans is of a Pacific origin owing to their more extended southern ranges along the North American west coast compared with the east coast. Although the general principle of this theory receives strong support from some other groups, particularly fishes, crustacea, and echinoderms (Ekman, 1953, p. 159), the distributions exhibited by most of the bryozoans

TABLE II. Southern ranges for cold-stenothermal bryozoans along the coast of northeastern America.

Hudson Strait	
Hincksina nigrans	*Hippoporina cancellata*
Bidenkapia spitzbergensis	*Schismopora nodulosa*
Reginella spitzbergensis	*Escharella connectens*
Escharoides jacksoni	*Smittina mucronata*
Harmeria scutulata	*Rhamphostomella hincksi*
Coastal Labrador	
Schizoporella obesa	
Gulf of St. Lawrence	
Membranipora serrulata	*Escharella thompsoni*
Terminoflustra membranaceotruncata	*Smittina groenlandica*
Doryporella spathulifera	*Porella aperta*
Microporina articulata	*Rhamphostomella plicata*
Membraniporella crassicosta	*Cheilopora sincera*
Stomachetosella limbata	*Phidolopora elongata*
Schizoporella stylifera	*Myriapora subgracila*
	Myriozoella plana
Southern Nova Scotia (including the Bay of Fundy and the northern part of the Gulf of Maine)	
Hincksipora spinulifera	*Cystisella saccata*
Kinetoskias arborescens	*Cystisella elegantula*
Stomachetosella hincksi	*Parasmittina jeffreysi*
Posterula sarsi	*Pseudoflustra solida*
Schizomavella porifera	*Rhamphostomella scabra*
	Lepraliella contigua
Cape Cod, Massachusetts	
Electra arctica	*Hippoporina reticulatopunctata*
Cauloramphus cymbaeformis	(Cape Anne, Mass.)
Tegella arctica	*Smittina majuscula*
Tegella armifera	*Rhamphostomella costata*
Stephanosella biaperta	*Rhamphostomella bilaminata*
Hippoporina propinqua	*Rhamphostomella ovata*

cited by Hansen are more adequately explained in terms of the uniformly low seasonal temperatures of North Pacific oceanic water.

ECOLOGY

A definite correlation between growth habit of the bryozoan colony and substrate type is demonstrated by some *Calanus* stations, although the absence of substrate data at others makes a comprehensive picture difficult to derive. As a general rule, however, the following species predominate on hard substrates: *Posterula sarsi*, *Celleporina surcularis*, *C. ventricosa*, *Cystisella saccata*, *Myriapora subgracila*. In all of these the mature colony is erect and rigid,

requiring firm anchorage on rocks or shells. Certain encrusting species exercise strong preferences for a hard substrate also, including *Electra arctica*, *Hincksipora spinulifera*, *Hippoporella hippopus*, and *Lepralia contigua*, whereas others, for example *Tegella arctica*, *T. armifera*, *Cribrilina annulata*, *Hippothoa hyalina*, *Harmeria scutulata*, and *Myriozoella plana*, are noted for their tolerance to both soft (algae and hydroids) and hard (rocks and shells) habitats.

Most arctic bryozoans are, in fact, adapted to a variety of substrate types; in the Cellularina for example, the erect flexible branching colony attaches with equal facility to rocks, shells, and hydroids alike, without any modification in growth habit. Other species which frequently encrust rocks or shells, e.g. *Bidenkapia spitzbergensis*, *Membraniporella crassicosta*, *Umbonula arctica*, *Schizomavella porifera*, *Hippoporina reticulatopunctata*, *Hippoporina propinqua*, *Cheilopora sincera* as well as some species of the genus *Rhamphostomella*, acquire a bilaminate foliaceous growth on hydroids, the branches of which become enveloped between the laminae. The tubelike habit of *Parasmittina jeffreysi* is also ideal for growth around hydroids stems, a habitat which is even occasionally chosen by the reteporid *Phidolopora elongata*, attachment being effected by the basal plate of kenozooids.

The most distinctive growth habit of all arctic bryozoans is exhibited by the genus *Pseudoflustra*, members of which possess a branching straplike bilamellar colony which (unlike other arctic species) is loosely attached to the substrate by long radicles, a type of growth rather similar to that of *Lanceopora*, a southwest Pacific genus.

According to the material furnished by four of the *Calanus* stations (three in Cresswell Bay, East Somerset Island; one in southeast Hudson Bay), *P. solida* apparently lives anchored directly to clay and mud substrates. In the Eurasian arctic on the other hand, Kluge (1962) recorded the species living attached to other bryozoans, annelid tubes, shells, and rocks. Presumably, the loosely attached growth habit enables this species to colonize both hard and soft substrates — an adaptation which may very well explain the extensive speciation of the genus in the Atlantic–arctic region.

Bryozoans were taken at five shore stations, including a suite of seven species at station 413 (Cumberland Sound). Only two species, however, have been recorded consistently in the intertidal zone of Baffin Island (Ellis, 1955). In arctic Canada, bryozoans mostly predominate at a depth of 30 m or below, i.e. beneath the zone of thermal warming effected by summer insolation (Ellis, 1960).

Although instances of specific bathymetric preference are not apparent in any of the fauna, some (eurythermal) species, including *Lichenopora hispida*, *L. verrucaria*, *Eucratea loricata*, *Cribrilina annulata*, and *Hippothoa hyalina*, commonly occurred in shallow waters (5–30 m), whereas others (panarctic), including *Reginella spitzbergensis*, *Escharoides jacksoni*, *Posterula sarsi*, *Celleporina ventricosa*, and *Pseudoflustra solida*, consistently indicated a deeper environment.

Breeding Seasons

There is a paucity of information relating to the breeding seasons of arctic bryozoans. MacGinitie (1955, p. 40) made the important observation that a large percentage of bryozoans at Point Barrow, Alaska, contain eggs during the winter (February) and suggested that these were produced from summer food reserves. Unfortunately, the *Calanus* and *Salvelinus* collections do not provide any new knowledge about the onset and termination of the arctic breeding season as all of the material was taken during successive summer seasons (June–September) when reproduction is most likely to occur.

SOME COMPARISONS BETWEEN THE BRYOZOAN FAUNAS OF THE ARCTIC AND ANTARCTIC REGIONS

One of the most outstanding features of the arctic bryozoan fauna concerns the impoverishment of indigenous taxa: few species occur exclusively in the arctic zone (high arctic, Ekman, 1953), certainly no genera. Seven genera on the other hand are presently recognized to be indigenous to the antarctic zone, three of which are speciose, i.e. *Camptoplites* (16 forms), *Cellariaeforma* (3 species), and *Cellarinella* (9 species). The fauna of the antarctic zone is also characterized by an exceptional richness of indigenous species. Rogick's (1965) checklist of bryozoans contained 179 indigenous forms, a figure which substantially exceeds that for the entire arctic region (157 forms[4]). The combined bryozoan fauna of the antarctic and subantarctic zones is approximately twice as large as that for the entire arctic region (cf. five times as large for the Echinodermata, Ekman, 1953, p. 227). Although there are no indigenous high-arctic genera, eight are recognized to be restricted exclusively to the panarctic area, two of which are speciose, i.e. *Pachyegis* (2 species), *Pseudoflustra* (5); the remainder are monotypic: (*Bidenkapia*, *Hincksipora*, *Harmeria*, *Cylindroporella*, *Posterula*, and *Myriozoella*).

As noted previously, the relationship between the distribution of bryozoans and the boundaries of arctic and subarctic zones of surface waters is not well shown. Hastings (1943), however, demonstrated a relationship between the range of some antarctic cellularine bryozoans and the position of the Antarctic Convergence Zone. The observation is an intriguing one, as there is little reason why benthic animals should correlate with surface water phenomena, unless influenced, as Fleming (1952, p. 118) suggested, "through differences in the "rain" of detrital plankton."

To date, the group has not furnished any significant evidence in support of the bipolar theory.

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[4]This figure includes 92 "purely arctic" forms listed by Borg (1933, p. 131) (reducible to 72 when synonyms and distributional data unavailable to Borg are evaluated); 11 new species from the western American subarctic (Osburn, 1950, 1952, 1953); and 74 forms from Soviet northern seas (Gostilovskaya, 1955, 1957; Kluge, 1946, 1952, 1953, 1955, 1962).

SYSTEMATICS

Order CYCLOSTOMATA

Family DIASTOPORIDAE

Genus *Diplosolen* Canu, 1918

Diplosolen obelia (Johnston, 1838)

Diastopora obelia Whiteaves, 1901, p. 112.

Diastopora obelia var. *arctica* Nordgaard, 1906, p. 36.

Diplosolen (Diastopora) obelium Osburn, 1923, p. 5D; 1932, p. 5; 1936, p. 540.

Diplosolen obelium Hutchins, 1940, p. 320.

Diplosolen obelia Hansen, 1962, p. 9; also var. *arctica* Kluge, 1962, p. 121, 122, text-fig. 53, 54; Powell, 1968.

Material examined. — stations 58, 406, 59-66, 61-39.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Victoria Island, (Hutchins); Foxe Basin, Hudson Strait (Osburn); Labrador (Kluge); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Santa Cruz, southern California; Jones Sound, Baffin Bay to Mount Desert Island, Maine. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 4–670 m.

Family IDMONEIDAE

Genus *Idmonea* Lamouroux, 1821

Idmonea atlantica Johnston, 1847

Idmonea pruinosa Stimpson, 1853, p. 18; Packard, 1863, p. 406.

Idmonea atlantica Packard, 1867, p. 270; Whiteaves, 1901, p. 111; Nordgaard, 1906, p. 26; Cornish, 1907, p. 78.

Tubulipora atlantica Osburn, 1912, p. 276.

Idomonea atlantica (sic) Osburn, 1923, p. 5D.

Idmidronea atlantica Hansen, 1962, p. 10.

Idmonea atlantica Kluge, 1962, p. 110, text-fig, 44; Powell, 1968.

Material examined. — stations 58, 221, 229, 61-43, 62-2012, 62-2031, 62-2032.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Dolphin and Union Strait (Osburn); Labrador (Kluge); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); off Cape Sable, N.S. (Osburn); Bay of Fundy (Stimpson, Powell). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to Cape Cod, Massachusetts; not known from the western American arctic area. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; British Isles; West Norway; Skagerrak; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Kurile Islands.

Bathymetric range: 5–2330 m.

Family LICHENOPORIDAE

Genus *Lichenopora* Defrance, 1823

Lichenopora hispida (Fleming, 1828)

Tubulipora crates Stimpson, 1853, p. 17.

Tubulipora hispida Packard, 1863, p. 406; 1867, p. 269.

Lichenopora hispida Whiteaves, 1901, p. 112; Osburn, 1923, p. 5D; 1932, p. 5.

Disporella hispida Hansen, 1962, p. 13.

Lichenopora hispida Powell and Crowell, 1967, p. 332; Powell, 1968.

Material examined. — stations 28, 203, 512, 609.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Hansen); Hudson Strait (Osburn); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Stimpson, Powell, and Crowell, 1967; Powell, 1968). (*b*) *Coastal North America*: Houston Stewart Channel, Queen Charlotte Islands to San Eugenio Point, California; Clarence Head, Baffin Bay to Biscayne Key, Florida. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; British Isles; West Norway; Skagerrak; Kattegat; Barents Sea; White Sea; Kara Sea.

Bathymetric range: 0–360 m.

Lichenopora verrucaria (Fabricius, 1780)

Diastopora verrucaria Packard, 1863, p. 406; 1867, p. 269.

Discoporella verrucaria Hincks, 1877a, p. 112.

Lichenopora verrucaria Whiteaves, 1901, p. 113; Nordgaard, 1906, p. 37; Cornish, 1907, p. 79; Osburn, 1912, p. 276; 1923, p. 5D; 1932, p. 5; 1936, p. 540; Hutchins, 1940, p. 31; Hansen, 1962, p. 13; Kluge, 1962, p. 169, text-fig. 84; Powell and Crowell, 1967, p. 332; Powell, 1968.

Material examined. — stations 58, 406.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Victoria Island (Hutchins); Dolphin and Union Strait, Fury and Hecla Strait, Frozen Strait, Hudson Bay and Strait, off Cape Sable, N.S. (Osburn); Labrador (Hincks, Kluge); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); Bay of Fundy (Powell and Crowell, 1967, Powell, 1968). (*b*) *Coastal North America*: Point Barrow, Alaska to San Miguel Island, southern California; Jones Sound, Baffin Bay to Long Island Sound, Connecticut. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; North Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chuckchi Sea; Sea of Okhotsk.

Bathymetric range: 0–700 m.

Order CTENOSTOMATA
Family ALCYONIDIIDAE
Genus *Alcyonidium* Lamouroux, 1812
Alcyonidium gelatinosum (Linnaeus, 1767)

Alcyonidium gelatinosum Whiteaves, 1901, p. 114; Osburn, 1932, p. 6; Ellis, 1955, p. 228, 230.

Material examined. — stations 103, 226, 413, 59-38, 59-40.

Distribution. — (*a*) *Canadian*: Hudson Strait (Osburn); Davis Strait (Ellis); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Orca, Gulf of Alaska to Vancouver Island; B.C., Hudson Strait to Mount Desert Island, Maine. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; British Isles; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; Kara Sea; East Siberian Sea; Chuckchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–475 m.

Order CHEILOSTOMATA
Suborder ANASCA Levinsen, 1909
Family SCRUPARIIDAE
Genus *Eucratea* Lamouroux, 1812
Eucratea loricata (Linnaeas, 1758)

Gemellaria dumosa Stimpson, 1853, p. 19.

Gemellaria loricata Hincks, 1877a, p. 110; Whiteaves, 1901, p. 91; Nordgaard, 1906, p. 6; Cornish, 1907, p. 75; Osburn, 1912, p. 277; 1923, p. 6D; 1932, p. 6; 1936, p. 541; Ellis, 1955, p. 228, 230.

Eucratea loricata Hansen, 1962, p. 14; also varieties Kluge, 1962, p. 261–264, text-fig. 147–150; Powell, 1968, p. 33.

Material examined. — stations 33, 53, 58, 225, 625, 815, 61-18, 61-43, 62-001, 62-032, 65-1048. N.M.C. Cat. No. 246; August 19, 1954; Ellef Ringnes Island, 46 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Dolphin and Union Strait, Foxe Channel, Hudson Bay and Strait (Osburn); Davis Strait (Ellis); Labrador (Hincks, Osburn, Kluge); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); Bay of Fundy (Stimpson, Powell). (*b*) *Coastal North America*: Isachsen, Ellef Ringnes Island to Masset Sound, Queen Charlotte Islands, B.C., Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Faeroes; British Isles; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–1359 m.

Family MEMBRANIPORIDAE
Genus *Membranipora* de Blainville, 1830
Membranipora serrulata (Busk, 1878)

Flustra serrulata Busk, 1878, p. 285; 1880, p. 234, pl. 13, fig. 2, 3, 4; Whiteaves, 1901, p. 95.
Membranipora serrulata Jullien and Calvet, 1903, p. 42, pl. 5, fig. 5.
Flustra serrulata Nordgaard, 1906, p. 9, pl. 1, fig. 6.
Membranipora serrulata Osburn, 1912, p. 279; 1923, p. 7D.
Membranipora serrullata (sic) Osburn, 1936, p. 541.
Membranipora serrulata Hansen, 1962, p. 14.

Material examined. — stations 58, 126, 201C, 221, 229, 331, 333, 723, 811, 821, 837, 61-18, 61-24, 61-26, 61-43, 62-033, 62-2031, 65-1506.

N.M.C. Cat. No. 249; August 4, 1939; Mouth of Lake Harbour, Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian* (*Fig. 2*): North Baffin Bay (Busk); Northwest Baffin Bay (Nordgaard, Osburn, Hansen); Dolphin and Union Strait, Fury and Hecla Strait, Foxe Channel, Labrador, Newfoundland (Jullien and Calvet, Osburn); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Franklin Pierce Bay, Kane Basin to the Gulf of St. Lawrence. Material from Liverpool Bay (*Salvelinus* station 62-033) comprises the first record of this species in the Beaufort Sea; not known from the eastern Pacific. (*c*) *Elsewhere*: West Greenland; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Kurile Islands.

Bathymetric range: 5–1267 m.

Family ELECTRINIDAE
Genus *Electra* Lamouroux, 1816
Electra arctica Borg, 1931

Electra crustulenta (Pallas) var. *arctica* Powell and Crowell, 1967, p. 338, pl. 1, fig. 2. (references); Powell, 1968.

Material examined. — stations 103, 106, 62-4305.

Remarks. — Except for Hansen (1962, p. 15) who considered *arctica* a subspecies of *E. crustulenta*, previous workers, including myself (Powell, 1967) have followed Borg's interpretation and treated his form as a variety of *crustulenta*. I am now of the opinion that the differences between the two forms, both morphological (the gymnocyst in *arctica* is much more extensive than that of *crustulenta*) as well as ecological (*crustulenta* is estuarine whereas *arctica* is stenohaline) are sufficient to recognize *arctica* as a valid species.

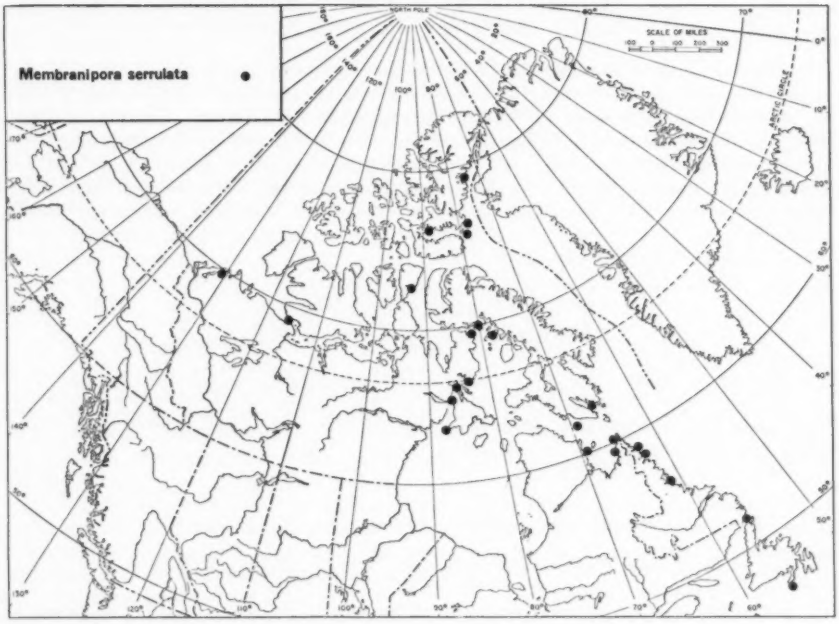

FIG. 2. Canadian distribution of *Membranipora serrulata*.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, 1906 as *Membranipora catenularia*); Hudson Strait (Osburn, 1932); Gulf of St. Lawrence (Whiteaves, 1901); Bay of Fundy (Stimpson, 1853; Powell and Crowell, 1967; Powell, 1968). (*b*)*Coastal North America*: Point Barrow, Alaska to Dillon Beach, California; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West Greenland; North Sea; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; Chukchi Sea; Sea of Okhotsk; Kurile Islands.

Bathymetric range: 0–520 m.

Family FLUSTRIDAE
Genus *Carbasea* Gray, 1848
Carbasea carbasea (Ellis and Solander, 1786)

Flustra digitata Packard, 1867, p. 274, pl. 7, fig. 16.

Flustra carbasea Whiteaves, 1901, p. 95; Osburn, 1912, p. 278.

Carbasea (*Flustra*) *carbasea* Osburn, 1932, p. 7.

Material examined. — stations 60-1001, 60-1035, 61-1015, 62-032.

Distribution. — (*a*) *Canadian*: Hudson Bay, Labrador (Osburn); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Point Barrow, Alaska; Hudson Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West Greenland; Jan Mayen Island; British Isles; North Sea; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 3–230 m.

Genus *Securiflustra* Silén, 1941
Securiflustra securifrons (Pallas, 1766)

Flustra securifrons Osburn, 1912, p. 278; 1932, p. 7; Kluge, 1962, p. 316, text-fig. 197.

Material examined. — stations 33, 103, 106, 231, 321, 322, 547, 837, 59-69, 61-43, 65-1506.

Distribution. — (*a*) *Canadian*: Hudson Bay, Newfoundland (Osburn); Labrador (Kluge). (*b*) *Coastal North America*: Frobisher Bay to Belle Isle Strait; not known from the western American arctic or eastern Pacific areas. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; North Sea; North Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–570 m.

Genus *Terminoflustra* Silén, 1941
Terminoflustra barleei (Busk, 1860)

Material examined. — N.M.C. Cat. No. 182; May 28, 1963; 51°22′N, 50°21′W; 366 m.

Distribution. — The present material now extends the recorded range of this species into the western Atlantic. *Elsewhere*: Faeroes; Shetland Islands; West Coast of Sweden; West and South Norway; Barents Sea.

Bathymetric range: 96–1100 m.

Terminoflustra membranaceotruncata (Smitt, 1867)

Flustra membranaceo-truncata Whiteaves, 1901, p. 94; Nordgaard, 1906, p. 9.

Material examined. — stations 547, 820, 59-68, 61-32.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Pribilof Islands, Bering Sea to Banks Island, Hecate Strait, B.C., Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 1–520 m.

Family HINCKSINIDAE
Genus *Hincksina* Norman, 1903a
Hincksina nigrans (Hincks, 1882) (Plate I, *d*)

Membranipora nigrans Nordgaard, 1906, p. 12, pl. 1, fig. 7–9.

Callopora nigrans Osburn, 1932, p. 8.

Material examined. — stations 20, 21, 33, 203, 723, 901, 60-1008, 62-009, 62-049, 62-4305.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Hudson Bay, Hudson Strait (Osburn). (*b*) *Coastal North America*: Point Barrow, Alaska to Houston Stewart Channel, Queen Charlotte Islands, B.C., Jones Sound, Baffin Bay to Ungava Bay. (*c*) *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–300 m.

Genus *Cauloramphus* Norman, 1903a
Cauloramphus cymbaeformis (Hincks)

Membranipora cymbaeformis Hincks, 1877a, p. 110.

Membranipora cymbiformis (sic) Hincks, 1888, p. 217, pl. 15, fig. 4; Whiteaves, 1901, p. 96.

Cauloramphus cymbaeformis Norman, 1903a, p. 588.

Membranipora cymbaeformis Nordgaard, 1906, p. 13; Osburn, 1912, p. 279.

Callopora cymbaeformis Osburn, 1923, p. 8D.

Cauloramphus cymbaeformis Osburn, 1932, p. 9; Hansen, 1962, p. 17; Powell, 1968.

Material examined. — stations 11, 58, 201C, 203, 226, 406, 553, 616.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Busk, Hansen); Hudson Bay, Hudson Strait (Osburn); Labrador (Hincks, Osburn); Gulf of St. Lawrence (Hincks, Whiteaves, Norman); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Icy Cape, Alaska; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–228 m.

Family ALDERINIDAE

Genus *Bidenkapia* Osburn, 1950

Bidenkapia spitzbergensis (Bidenkap, 1897) (Plate I, *a*, *b*)

The following references pertain to arctic North America.

Callopora spitzbergensis Osburn, 1923, p. 8D; 1932, p. 8.

Bidenkapia spitzbergensis; also var. *alaskensis* Osburn, 1950, p. 76, 77; pl. 8, fig. 6, 7.

Material examined. — stations 13, 20, 21, 28, 30, 33, 58, 126, 201C, 221, 226, 406, 837, 61-26, 61-43.

Distribution. — (*a*) *Canadian*: Hudson Strait (Osburn). (*b*) *Coastal North America* (*Fig. 3*): Point Barrow, Alaska to Punuk Island, Bering Sea; Frobisher Bay to Hudson Strait. (*c*) *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; White Sea; Kara Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–1000 m.

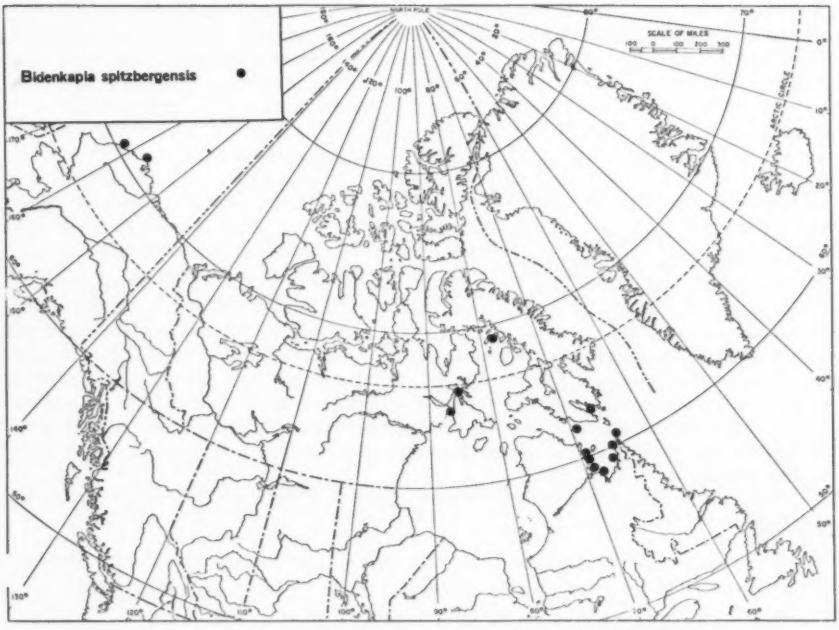

FIG. 3. North American distribution of *Bidenkapia spitzbergensis*.

Genus *Callopora* Gray, 1848
Callopora lineata (Linnaeus, 1767)

Membranipora lineata Packard, 1863, p. 408; 1867, p. 272; Hincks, 1877a, p. 110; Whiteaves, 1901, p. 96; Cornish, 1907, p. 76.

Callopora lineata Osburn, 1923, p. 7D; 1932, p. 8; 1936, p. 541; Hutchins, 1940, p. 32; Kluge, 1962, p. 287, text-fig. 70.

Material examined. — station 61-63.

Distribution. — (*a*) *Canadian*: Dolphin and Union Strait (Osburn, Hutchins); Frozen Strait, Hudson Bay, Hudson Strait (Osburn); Labrador (Hincks, Kluge); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish). (*b*) *Coastal North America*: Nunivak Island, Bering Sea to Santa Cruz Island, southern California; Hudson Strait to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–378 m.

Callopora craticula (Alder, 1857)

Membranipora craticula Whiteaves, 1901, p. 96.

Callopora craticula Norman, 1903a, p. 589.

Membranipora craticula Nordgaard, 1906, p. 10; Osburn, 1912, p. 278.

Callopora craticula Osburn, 1923, p. 8D; 1932, p. 7; 1936, p. 541; Powell, 1968.

Material examined. — stations 53, 58, 126, 226, 553, 608.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Dolphin and Union Strait, Frozen Strait, Hudson Bay, Hudson Strait, Labrador, Newfoundland (Osburn); Gulf of St. Lawrence (Norman, Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to Long Island Sound, Connecticut. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–280 m.

Genus *Copidozoum* Harmer, 1926
Copidozoum smitti (Kluge, 1946) (Plate I, *c*)

Callopora smitti Kluge, 1962, p. 291, text-fig. 174.

Material examined. — station 413.

Description (translated from the Russian: Kluge, 1962, p. 291). — "Colony encrusting; zooids arranged in straight or oblique rows. Aperture oval, long and narrow or short and broad with a raised margin, the cryptocyst in the form of a narrow fringe. Nine to fourteen spines occur around the apertural margin, straight or weakly inclined over the aperture. Ovicells small, rounded, the frontal surface granular. Avicularia large, vicarious with a long pointed mandible, almost as large as the zooids; also small, adventitious, occurring on the gymnocyst below the proximal margin of the aperture, the mandible directed proximally. The avicularia are seen most frequently on fertile zooids at the distal margin of the ovicell, the mandible being directed either distally, or disto-laterally.

The species occurs on hydroids, shells and stone at a depth of 23.5–130 metres, on rock, sand and silt."

Remarks. — The large, acutely triangle-shaped rostrum of the vicarious avicularium (Plate I, *c*) is a diagnostic character of the genus *Copidozoum*, to which the present species is now referred.

Kluge (p. 292) considered that Osburn's (1923, 1932) records of *Callopora discreta* (Hincks) from Dolphin and Union Strait and Hudson Strait pertain to *C. smitti*, an opinion that I have been unable to verify.

Distribution. — West Greenland; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea.

Genus *Tegella* Levinsen, 1909
Tegella arctica (d'Orbigny, 1851)

Membranipora sophiae Whiteaves, 1901, p. 96.
Callopora sophiae Norman, 1903a, p. 590.
Membranipora arctica Nordgaard, 1906, p. 10.
Callopora arctica Osburn, 1932, p. 7.
Tegella arctica Powell and Crowell, 1967, p. 341.
Material examined. — stations 203, 406, 723, 805, 821.
Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Hudson Strait (Osburn); Gulf of St. Lawrence (Whiteaves, Norman); Bay of Fundy (Powell and Crowell). (*b*) *Coastal North America*: Point Barrow, Alaska to Houston Stewart Channel, Queen Charlotte Islands, B.C., Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; West Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Sea of Okhotsk.
Bathymetric range: 0–300 m.

Tegella armifera (Hincks, 1880) (Plate II, *a*)

Membranipora armifera Hincks, 1892, p. 155, pl. 8, fig. 4.
Membranipora sophiae var. *armifera* Whiteaves, 1901, p. 97.
Callopora unicornis var. *armifera* Norman, 1903a, p. 591, pl. 13, fig. 10, 11.
Membranipora unicornis var. *armifera* Nordgaard, 1906, p. 11.
Tegella unicornis var. *armifera* Osburn, 1923, p. 9D; 1932, p. 90.
Tegella armifera Powell and Crowell, 1967, p. 340; Powell, 1968.
Material examined. — stations 11, 28, 33, 203, 226, 413, 553, 611, 61-11, 62-049, 62-2014. N.M.C. Cat. No. 243; August 19, 1954; Ellef Ringnes Island, 46 m.
Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Dolphin and Union Strait, Hudson Bay, Hudson Strait (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves, Norman); Bay of Fundy (Powell and Crowell, 1967; Powell, 1968). (*b*) *Coastal North America*: Isachsen, Ellef Ringnes Island to San Pedro, California; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.
Bathymetric range: 0–314 m.

Genus *Doryporella* Norman, 1903b
Doryporella spathulifera (Smitt, 1867) (Plate II, *b*)

Lepralia spathulifera Whiteaves, 1901, p. 101.
Doryporella spatulifera (sic) Norman, 1903b, p. 106.
Doryporella spathulifera Nordgaard, 1906, p. 14.
Lepralia spathulifera Osburn, 1912, p. 282, pl. 34, fig. 2*a*, *b*.
Material examined. — stations 33, 103, 413, 616.
Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); St. Pierre Bank, Newfoundland (Osburn); Gulf of St. Lawrence (Whiteaves, Norman). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West

and East Greenland; Iceland, Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–300 m.

Family MICROPORIDAE

Genus *Microporina* Levinsen, 1909

Microporina articulata (Fabricius, 1824) (Plate II, *c*, *d*)

Cellaria articulata Nordgaard, 1906, p. 8.

Microporina borealis Osburn, 1932, p. 12; 1936, p. 541.

Material examined. — stations 33, 58, 221, 225, 229, 317, 321, 512, 805, 61-24, 65-1506.

N.M.C. Cat. No. 248; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn); Fury and Hecla Strait, Foxe Channel, Hudson Strait (Osburn). (*b*) *Coastal North America*: Point Barrow, Alaska to Snake Island (Vancouver Island, B.C.); Coburg Island, Baffin Bay to Belle Isle Strait. (*c*) *Elsewhere*: West Greenland; Spitsbergen; Barents Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 6–500 m.

Family SCRUPOCELLARIIDAE

Genus *Scrupocellaria* Van Beneden, 1845

Scrupocellaria arctica (Busk, 1855) (Plate III, *f*)

Material examined. — station 58.

Distribution. — The *Calanus* material comprises a new record for this species in the Canadian area. *Elsewhere*: West Greenland; Barents Sea; White Sea; Kara Sea; Bering Sea; Sea of Okhotsk.

Bathymetric range: 0–308 m.

Scrupocellaria scabra (van Beneden, 1848) (Plate III, *b*, *c*, *e*)

Scrupocellaria scabra Busk, 1878, p. 283; 1880, p. 231; Hincks, 1889, p. 427, pl. 21, fig. 1; Whiteaves, 1901, p. 93; Nordgaard, 1906, p. 7; Osburn, 1912, p. 277; 1923, p. 7D.

Scrupocellaria scabra var. *paenulata* Osburn, 1932, p. 11.

Scrupocellaria scabra Osburn, 1936, p. 541; Hansen, 1962, p. 22; Powell, 1968.

Material examined. — stations 225, 319, 331, 608, 723, 58-3, 58-33, 62-4304, 65-1502.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Busk, Osburn, Hansen); Dolphin and Union Strait, Hudson Bay and Strait (Osburn); Labrador (Busk); Newfoundland (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow to Alitak Bay, Alaska; Franklin Pierce Bay, Kane Basin to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; British Isles; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–454 m.

Genus *Caberea* Lamouroux, 1816

Caberea ellisii (Fleming, 1828) (Plate III, *a*)

Caberea hookeri Packard, 1863, p. 409; 1867, p. 273.

Caberea ellisii Whiteaves, 1901, p. 93; Cornish, 1907, p. 76; Osburn, 1912, p. 277; 1932, p. 12; Powell, 1968.

Material examined. — stations 221, 520.

N.M.C. Cat. No. 250; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: Hudson Bay (Osburn); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); off Cape Sable, N.S. (Osburn); Bay of

Fundy (Powell). (*b*) *Coastal North America*: Icy Cape, Alaska to San Benito Island, southern California; Hudson Strait to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West Greenland; Iceland; Faeroes; British Isles; West Norway; Spitsbergen; Barents Sea; White Sea; Chukchi Sea.

Bathymetric range: 9–432 m.

Genus *Notoplites* Harmer, 1923
Notoplites smitti (Norman, 1868) (Plate III, *g*)

Menipea smitti Osburn, 1923, p. 7D.

Material examined. — station 65-1044.

Distribution. — Not known in the western American arctic or the eastern Pacific. (*a*) *Canadian*: Dolphin and Union Strait. (*b*) *Elsewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea.

Bathymetric range: 1–698 m.

Genus *Tricellaria* Fleming, 1828
Tricellaria ternata (Ellis and Solander, 1786)

Cellularia ternata Stimpson, 1853, p. 19.

Menipea ternata Packard, 1863, p. 409; 1867, p. 273; Hincks, 1877a, p. 110; Whiteaves, 1901, p. 92; Cornish, 1907, p. 75; Osburn, 1912, p. 277.

Tricellaria (*Menipea*) *ternata* Osburn, 1932, p. 11.

Tricellaria ternata Kluge, 1962, p. 274, text-fig. 235; Powell, 1968.

Material examined. — stations 33, 225, 547, 61-43, 65-1505, 65-1510.

Distribution. — (*a*) *Canadian*: Hudson Strait (Osburn); Labrador (Hincks, Osburn, Kluge); Strait of Belle Isle (Packard); Newfoundland (Osburn); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); off Cape Sable, N.S. (Osburn); Bay of Fundy (Stimpson, Powell). (*b*) *Coastal North America*: Yakutat, Gulf of Alaska to Lands End, California; Hudson Strait to Long Island Sound, Connecticut. (*c*) *Elsewhere*: West and East Greenland; Iceland, Jan Mayen Island; Faeroes; British Isles; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–366 m.

Tricellaria gracilis (van Beneden, 1848) (Plate III, *d*)

Menipea gracilis Busk, 1878, p. 284; 1880, p. 232; Nordgaard, 1906, p. 6.

Tricellaria ternata var. *gracilis* Osburn, 1932, p. 12; 1936, p. 541.

Tricellaria gracilis Hansen, 1962, p. 21.

Tricellaria gracilis; also var. *inermis* Kluge, 1962, p. 375 and 376; text-fig. 236, 237.

Material examined. — stations 58, 221, 232, 61-26,
N.M.C. Cat. No. 245; August 19, 1954; Ellef Ringnes Island, 46 m.

Remarks. — The material from Ellef Ringnes Island (Plate III, *d*,) is without frontal scutes and lateral avicularia, thereby resembling the variety *inermis* of Kluge.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk); Northwest Baffin Bay (Nordgaard, Hansen, Osburn); Foxe Channel, Hudson Bay, Hudson Strait (Osburn); Labrador (Kluge); Gulf of St. Lawrence (Kluge). (*b*) *Coastal North America*: Isachsen, Ellef Ringnes Island to southern Vancouver Island, B.C., Franklin Pierce Bay, Kane Basin to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Skagerrak; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–869 m.

Tricellaria peachii (Busk, 1851) (Plate III, *h*)

Cellularia peachii Packard, 1863, p. 409; 1867, p. 272; Hincks, 1877a, p. 110; 1888, p. 216, pl. 15, fig. 6; Whiteaves, 1901, p. 92.

Tricellaria (*Cellularia*) *peachi* Osburn, 1932, p. 12.

Tricellaria (*Bugulopsis*) *peachi* Osburn, 1936, p. 541.

Tricellaria peachi Hansen, 1962, p. 21.

Bugulopsis peachi Kluge, 1962, p. 367, text-fig. 229.

Material examined. — stations 33, 719, 59-21, 59-50, 61-10, 61-43.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Hansen); Fury and Hecla Strait, Hudson Bay (Osburn); Labrador (Hincks, Kluge); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Hincks, Whiteaves). (*b*) *Coastal North America*: Clarence Head, Baffin Bay to Cape Cod, Massachusetts; not known from the western American arctic or eastern Pacific areas. (*c*) *Elsewhere*: West and East Greenland; Iceland; British Isles; West Norway; Finmark; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–475 m.

Family BICELLARIELLIDAE

Genus *Dendrobeania* Levinsen, 1909

Dendrobeania murrayana (Johnston, 1847)

Menipea fruticosa Packard, 1863, p. 409, pl. 1, fig. 3.

Flustra murrayana Packard, 1863, p. 410.

Menipea fruticosa Packard, 1867, p. 273.

Bugula murrayana Packard, 1867, p. 274; Busk, 1878, p. 284.

Bugula fruticosa Busk, 1878, p. 285.

Bugula murrayana Busk, 1880, p. 233.

Bugula fruticosa Busk, 1880, p. 233, pl. 13, fig. 1.

Bugula murrayana Whiteaves, 1901, p. 93; Nordgaard, 1906, p. 7.

Bugula murrayana var. *fruticosa* Nordgaard, 1906, p. 8.

Bugula murrayana Osburn, 1912, p. 277.

Dendrobeania murrayana var. *fruticosa* Osburn, 1923, p. 6D.

Dendrobeania murrayana var. *quadridentata* Osburn, 1923, p. 7D.

Dendrobeania (*Bugula*) *murrayana* var. *fruticosa* Osburn, 1932, p. 11.

Dendrobeania (*Bugula*) *murrayana* var. *quadridentata* Osburn, 1932, p. 11.

Dendrobeania murrayana var. *fruticosa* Osburn, 1936, p. 541.

Dendrobeania murrayana Hansen, 1962, p. 25; Powell, 1968.

Material examined. — stations 33, 321, 322, 608, 611, 828, 901, 61-1, 61-18, 65-1502, 65-1505, 65-1510.

Remarks. — This is a highly variable species, *Calanus* material being represented mainly by the varieties *fruticosa* (Packard) and *quadridentata* (Loven), although the variety *frigida* (Waters) (see Kluge, 1962, text-fig. 208) was also recognized.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk); Northwest Baffin Bay (Nordgaard, Hansen); Dolphin and Union Strait, Frozen Strait, Hudson Bay and Strait, Labrador (Osburn); Strait of Belle Isle (Packard); off Cape Sable, N.S. (Osburn); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Puget Sound, Washington; Franklin Pierce Bay, Kane Basin to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; West Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–753 m.

Genus *Kinetoskias* Danielssen, 1868
Kinetoskias arborescens Danielssen, 1868

Kinetoskias arborescens Whiteaves, 1901, p. 94; Osburn, 1912, p. 278.

Material examined. — stations 33, 59-6, 63-019.

N.M.C. Cat. No. 239; August 27, 1952; Prince Patrick Island, 30–45 m.

Distribution. — (*a*) *Canadian*: Gulf of St. Lawrence (Whiteaves); off Cape Sable, N.S., Sable Island, N.S. (Osburn). (*b*) *Coastal North America*: Mould Bay, Prince Patrick Island; Hudson Strait to Cape Sable, N.S.; not known from the western American arctic or the eastern Pacific. (*c*) *Elsewhere*: East Greenland; West Norway; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea.

Bathymetric range: 18–1229 m.

Family CRIBRILINIDAE
Genus *Cribrilina* Gray, 1848
Cribrilina annulata (Fabricius, 1780)

Lepralia annulata Stimpson, 1853, p. 18; Packard, 1863, p. 406; 1867, p. 270; Hincks, 1877a, p. 110.

Cribrilina annulata Whiteaves, 1901, p. 98; Nordgaard, 1906, p. 13; Cornish, 1907, p. 77; Osburn, 1912, p. 279; 1923, p. 9D; 1932, p. 9; 1936, p. 541; Powell, 1967, p. 1905, fig. 1, 2; Powell and Crowell, 1967, p. 341.

Material examined. — stations 33, 723.

Remarks. — The occurrence in this species of adventitious gonozoids which are budded off from frontal dietellae, was discussed by Powell (1967). No gonozooids were observed in any of the *Calanus* material, however.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Dolphin and Union Strait, North Somerset Island, Frozen Strait, Hudson Strait, (Osburn); Labrador (Hincks); Strait of Belle Isle (Packard); Gulf of St, Lawrence (Whiteaves, Powell); off Canso, N.S., off Cape Sable, N.S. (Cornish, Osburn); Bay of Fundy (Stimpson Powell, and Crowell). (*b*) *Coastal North America*: Point Barrow, Alaska to southern Vancouver Island, B.C., Jones Sound, Baffin Bay to Nantucket Island, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; British Isles; North Sea; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–112 m.

Genus *Membraniporella* Smitt, 1873
Membraniporella crassicosta Hincks, 1888 (Plate IV, *b*)

The following references pertain to arctic North America:

Membraniporella crassicosta Hincks, 1888, p. 216, pl. 14, fig. 5; Whiteaves, 1901, p. 98; Osburn, 1912, p. 279; 1950, p. 176, pl. 27, fig. 1, 2.

Material examined. — stations 33, 226, 331, 406, 65-1510.

Remarks. — The frontal shield in this species exhibits a remarkable degree of variation. In some zooids the mode of fusion of the overarching spines (see Osburn, 1950, pl. 27, fig. 2) accords closely with that described for other species of the genus. Usually, however, development of the shield is incomplete (Plate IV, *b*), the incipient spines being compressed and massive or sometimes wanting altogether. As with most other species of *Membraniporella* (Cook, 1967, p. 329) communication pores in *crassicosta* comprise septulae,

one occurring on each distal-lateral wall, also one on the distal wall. Unlike others, however, larval incubation apparently takes place within the zooecium, as ovicells have not been found in Hincks' species to date.

Distribution. — Collecting to date has failed to establish the occurrence of this species in the central Canadian and Eurasian arctic areas. Evidence for a much wider distribution is therefore required before *M. crassicosta* can be considered "probably circumpolar" (Osburn, 1950, p. 177), its present pattern of distribution conforming to the type Ekman (1953, p. 180) termed "discontinuous circumpolar" (Fig. 4).

Bathymetric range: 18–100 m.

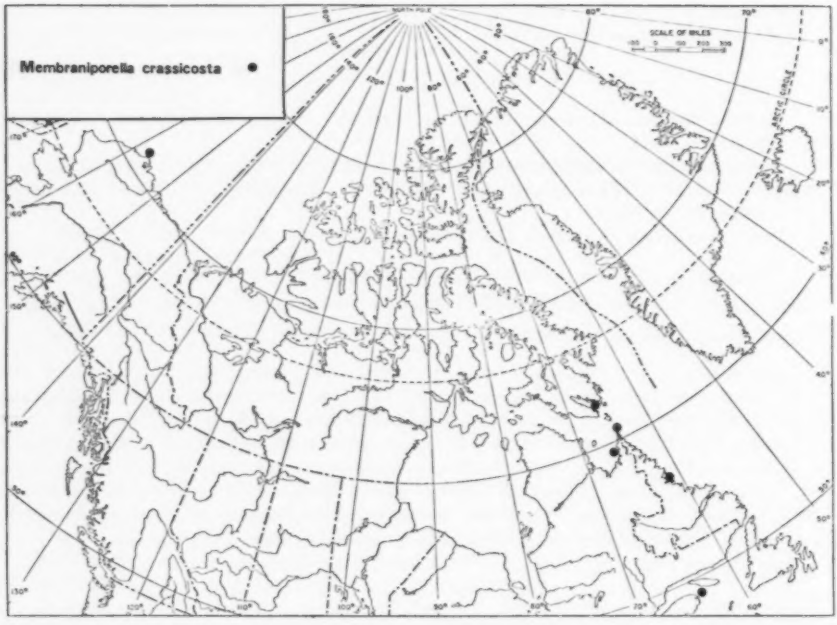

FIG. 4. Total distribution of *Membraniporella crassicosta*.

Genus *Reginella* Jullien, 1886

Reginella spitzbergensis (Norman, 1903b) (Plate IV, *a*)

Material examined. — stations 102, 103, 126, 231, 334.

Distribution. — The *Calanus* material extends the recorded latitudinal range of this species southwards into the subarctic (Fig. 5), constituting a new record for the Canadian area. *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Beaufort Sea.

Bathymetric range: 28–327 m.

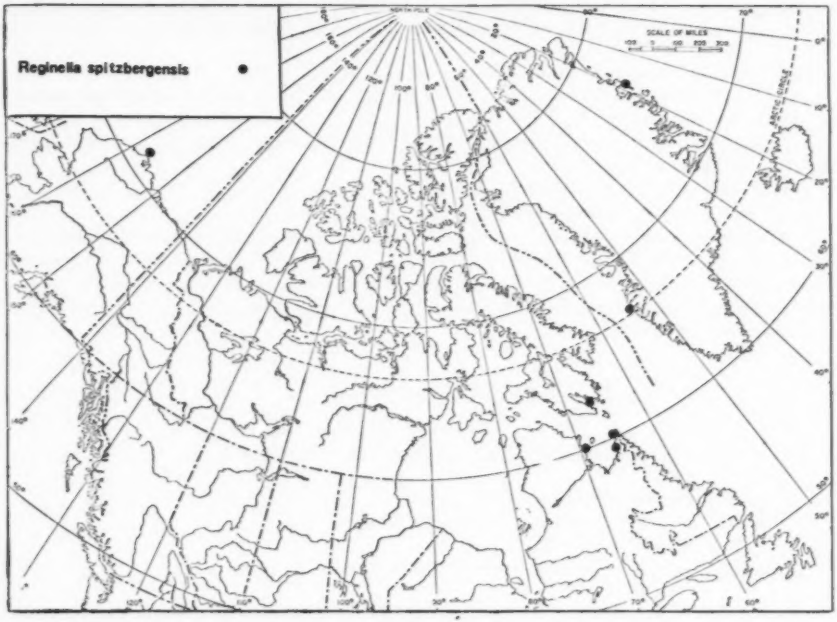

FIG. 5. Distribution of *Reginella spitzbergensis* in North America and Greenland.

Suborder ASCOPHORA Levinsen, 1909
Division I *ASCOPHORA IMPERFECTA* Harmer, 1957
HINCKSIPORIDAE new family

Diagnosis. — Encrusting Ascophora with a greatly thickened frontal shield perforated by a few small marginal pores. Orifice somewhat variable, subquadrate to transversely ovate, the proximal lip frequently bearing a small spine. Ovicell entozooecial. Spines and avicularia wanting.

Remarks. — The development of the frontal shield in *Hincksipora* is of the umbonuloid type, overarching an extensive frontal membrane to which is fused the operculum (Osburn, 1952, p. 284). These features signify a strong relationship with the Ascophora Imperfecta. Tentatively assigned to the Hippothoidae by Osburn (1952), the differences of morphology between *Hincksipora* and *Hippothoa* are so great that a new family is here proposed to accomodate the former genus.

Genus *Hincksipora* Osburn, 1952

Remarks. — It is advisable to point out that the genus *Escharelloides* of Kluge (1962, p. 412) is not valid because of Osburn's (1952, p. 282) prior selection of *Mucronella spinulifera* Hincks, as the type of *Hincksipora*.

Hincksipora spinulifera (Hincks) (Plate 5, *d*)

Mucronella spinulifera Hincks, 1889, p. 431, pl. 21, fig. 3.

Not *Monoporella spinulifera* var. *praeclara* Hincks, 1892, pl. 8, fig. 3. (= *Pachyegis producta* (Packard) see footnote, p. 49.)

Monoporella spinulifera Whiteaves, 1901, p. 108; Norman, 1903b, p. 115; Nordgaard, 1906, p. 26; Osburn, 1912, p. 282.

Mucronella spinulifera Osburn, 1912, p. 282.

Material examined. — stations 33, 103, 106, 208, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Labrador (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves, Norman). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to Mount Desert Island, Maine. (*c*) *Elsewhere*: West Greenland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea.

Bathymetric range: 8–186 m.

Family UMBONULIDAE

Genus *Umbonula* Hincks, 1880

Umbonula arctica (M. Sars, 1851) (Plate V, *a*)

Mucronella pavonella Whiteaves, 1901, p. 107.

Discopora (*Mucronella*) *pavonella* Nordgaard, 1906, p. 23.

Umbonula arctica Powell, 1968.

Material examined. — stations 33, 201C, 203, 226, 547, 723, 61-26.

Remarks. — Unlike other representatives of the genus *Umbonula*, ovicells have never been observed in this species, larval incubation apparently taking place within the zooecia.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Puget Sound, Washington; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Sea; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 1–345 m.

Genus *Escharoides* Milne-Edwards, 1836

Escharoides jacksoni (Waters, 1900) (Plate V, *b*)

Escharoides jacksoni Nordgaard, 1906, p. 27.

Peristomella (*Escharoides*) *jacksoni* Osburn, 1923, p. 10D; 1932, p. 13.

Material examined. — stations 820, 837, 61-10, 61-34, 61-39, 62-2012, 62-2014, 62-2031, 62-2032.

N.M.C. Cat. No. 242; August 19, 1954; Ellef Ringnes Island, 46 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Dolphin and Union Strait, Hudson Strait (Osburn). (*b*) *Coastal North America* (Fig. 6): Isachsen, Ellef Ringnes Island to Point Barrow, Alaska; Jones Sound, Baffin Bay to Hudson Strait. (*c*) *Elsewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Sea of Okhotsk.

Bathymetric range: 0–1000 m.

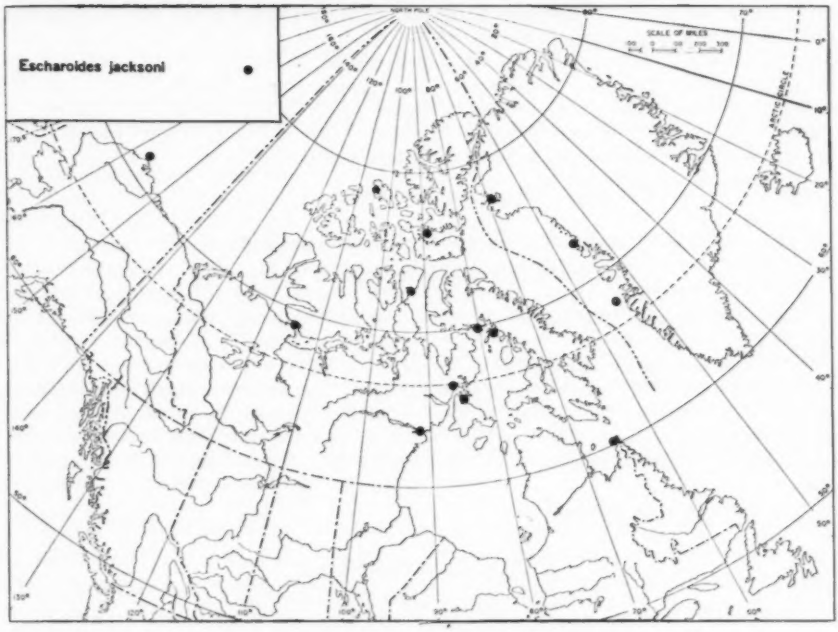

FIG. 6. Distribution of *Escharoides jacksoni* in North America and West Greenland.

Division II *ASCOPHORA VERA* Harmer, 1957
Family HIPPOTHOIDAE
Genus *Hippothoa* Lamouroux, 1821
Hippothoa expansa Dawson, 1859

Hippothoa expansa Dawson, 1859, p. 256; Packard, 1863, p. 406; 1867, p. 270; Whiteaves, 1901, p. 101; Nordgaard, 1906, p. 14; Osburn, 1932, p. 12; Hansen, 1962, p. 27.

Material examined. — stations 28, 106, 206, 208, 616, 59-21, 61-12, 65-1506.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Nordgaard); Northwest Baffin Bay (Nordgaard, Hansen); Hudson Strait (Osburn); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Dawson, Whiteaves). (*b*) *Coastal North America*: Point Barrow, Alaska to Santa Rosa Island, southern California; Smith Sound, Baffin Bay to Mount Desert Island, Maine. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Kurile Islands; Sea of Japan.

Bathymetric range: 18–672 m.

Hippothoa hyalina (Linnaeus, 1767)

Lepralia hyalina Hincks, 1877a, p. 110.

Schizoporella hyalina Whiteaves, 1901, p. 100.

Hippothoa hyalina Nordgaard, 1906, p. 14.

Schizoporella hyalina Cornish, 1907, p. 77.

Hippothoa hyalina Osburn, 1912, p. 280; 1923, p. 9D; 1932, p. 12; 1936, p. 541; Hutchins, 1940, p. 32; Powell and Crowell, 1967, p. 342; Powell, 1968.

Material examined. — stations 11, 20, 21, 28, 33, 58, 106, 203, 318, 406, 512, 547, 609, 613, 614, 723, 805, 821, 901, 62-032, 62-2002, 62-4305.

Distribution. — (*a*) *Canadian*: North and northwest Baffin Bay (Nordgaard); Victoria Island, (Hutchins); Fury and Hecla Strait, Foxe Channel, Hudson Bay and Strait (Osburn); Labrador (Hincks, Osburn); Newfoundland (Osburn); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell and Crowell). (*b*) *Elsewhere*: Widely distributed in arctic and boreal waters.

Bathymetric range: 0–2018 m.

Genus *Harmeria* Norman, 1903a
Harmeria scutulata (Busk, 1855)

Harmeria scutulata Nordgaard, 1906, p. 14; Osburn, 1923, p. 9D; 1932, p. 12; 1936, p. 541; Hutchins, 1940, p. 33.

Material examined. — station 208.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Victoria Island, (Hutchins); Dolphin and Union Strait, Hudson Strait, Frozen Strait (Osburn). (*b*) *Coastal North America*: Punuk Island, Bering Sea; Jones Sound, Baffin Bay to Hudson Strait. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea.

Bathymetric range: 0–90 m.

Family GIGANTOPORIDAE
Genus *Cylindroporella* Hincks, 1877a
Cylindroporella tubulosa (Norman, 1868)

Porina tubulosa Whiteaves, 1901, p. 98; Nordgaard, 1906, p. 14.

Cylindroporella tubulosa Osburn, 1923, p. 11D.

Cylindroporella (*Porina*) *tubulosa* Osburn, 1932, p. 12.

Material examined. — stations 413, 58-3.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Dolphin and Union Strait, Hudson Strait (Osburn); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Point Barrow, Alaska to Point Etches, Queen Charlotte Islands, B.C., Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Faeroes; Shetland Islands; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–230 m.

Family STOMACHETOSELLIDAE
Genus *Stomachetosella* Canu and Bassler, 1917
Stomachetosella cruenta (Busk, 1854) (Plate VI, *b*)

Schizoporella cruenta Hincks, 1892, p. 153, pl. 8, fig. 5; Whiteaves, 1901, p. 100; Nordgaard, 1918, p. 56–57.

Material examined. — stations 33, 203, 58-3, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Hincks, Whiteaves). (*b*) *Coastal North America*: Cape Lisburne, Alaska to Puget Sound, Washington; Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West Greenland; Jan Mayen Island; British Isles; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 6–324 m.

Stomachetosella hincksi n.sp. (Plate VI, *a*)

Smittia producta Hincks, 1889, p. 430, pl. 21, fig. 2; Whiteaves, 1901, p. 106 (not of Packard, 1863).

Schizoporella producta Nordgaard, 1906, p. 19, pl. 2, fig. 19–21 (not of Packard).

Stomachetosella producta Osburn, 1933, p. 36, pl. 15, fig. 1–3; Hansen, 1962, p. 29; Kluge, 1962, p. 504, text-fig. 350 (not of Packard).

Material examined. — stations 65-1505, 65-1506.

Holotype: N.M.C Cat. No. 756. *Calanus* Station 65-1505, Strait of Belle Isle (mounted slide, Plate VI, *a*).

Diagnosis. — Encrusting *Stomachetosella* with a greatly thickened, conspicuously perforated frontal wall. Primary orifice deeply immersed. Secondary orifice pyriform. Ovicell imperforate, recumbent. No avicularia or spines.

Description. — *Colony* robust, encrusting, coloured reddish-brown in fresh material. *Zooids* large, roundly hexagonal, irregularly arranged in diverging rows, separated by thickened septal walls. *Primary orfice* deeply immersed, arched distally, the proximal lip concave, with a small cardelle at each corner. *Secondary orfice* pyriform, rounded distally, narrowing proximally and forming a distinct notch. *Frontal wall* greatly thickened, weakly convex, densely granular, perforated by several prominent pores. *Ovicell* hyperstomial, rounded, imperforate, immersed in older areas of the colony. *Pore chambers*: 2–3 on the distal wall, 3–4 on each disto-lateral wall. Oral spines and avicularia wanting.

Remarks. — The robust construction of the frontal wall is well illustrated in Osburn (1933, pl. 15, fig. 2). Encroachment by the frontal walls of adjoining zooids frequently conceals the ovicell, particularly in older areas of the colony.

Owing to the inadequacy of Packard's description, Hincks (1889, p. 430) remained uncertain as to the proper identity of the Gulf of St. Lawrence material that he assigned to *Smittia producta* (Packard). After examining Packard's material from Caribou Island, Belle Isle Strait (M.C.Z.) in some detail, I have concluded that *Lepralia producta* Packard (1863) was based on two species, neither of which are related to Hincks' (1889) material of that name.

The first species, i.e. *Lepralia producta sensu stricto*, comprises extremely large individuals coloured reddish-brown. The orifice is horseshoe shaped, the frontal wall being heavily calcified with extensive perforations.[5] Five such zooids were illustrated by Packard (1863, pl. 2) on the left side of his fig. 1. Norman's (1903b, p. 114, pl. 9, fig. 8–11) description and figures of *Porella princeps* from West Greenland leave no doubt that his species is the same as Packard's material, and must therefore, take Packard's earlier specific name. The proper identity of *Lepralia producta* becomes particularly important in view of Osburn's selection of *Porella princeps* as the type of the genus *Pachyegis*. *Pachyegis producta* is not represented amongst the collections dealt with in this report, but a photomicrograph of Packard's type material is provided here for comparison (Plate V, *c*). According to MacGinitie (1955, p. 132) this "is the most abundant and conspicuous encrusting species at Point Barrow," Alaska.

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[5]Material from the Gulf of St. Lawrence assigned by Hincks (1892, p. 152, pl. 8, fig. 3) to "*Monoporella spinulifera* var. *praeclara*" is conspecific with this species.

The second, smaller species which Packard (p. 407) interpreted as a juvenile stage of the above species and portrayed as three individuals on the right side of his fig. 1 (plate 2) is really *Smittina bella* (Busk) (q.v.).

Stomachetosella hincksi is named for its discoverer, the late Reverend T. H. Hincks, F.R.S.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Gulf of St. Lawrence (Hincks, Whiteaves). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to Mount Desert Island, Maine; not known from the western American arctic or the eastern Pacific. (*c*) *Elsewhere*: West Greenland; Barents Sea; Chukchi Sea.

Bathymetric range: 23–672 m.

Stomachetosella limbata (Lorenz, 1886)

Schizoporella levinseni Nordgaard, 1906, p. 18.

Schizoporella limbata Kluge, 1962, p. 488, text-fig. 334.

Material examined. — stations 106, 208, 319, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Kluge). (*b*) *Coastal North America*: Gabriola Pass, Vancouver Island, B.C., Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elswhere*: West Greenland; Jan Mayen Island; North Norway; Barents Sea; White Sea; Kara Sea; Laptev Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 20–315 m.

Stomachetosella sinuosa (Busk, 1860)

Schizoporella sinuosa Whiteaves, 1901, p. 100; Cornish, 1907, p. 77; Osburn, 1923, p. 9D; 1932, p. 13.

Stomachetosella sinuosa Powell, 1968.

Material examined. — stations 106, 208.

Distribution. — (*a*) *Canadian*: Dolphin and Union Strait, Hudson Strait (Osburn); Gulf of St. Lawrence (Whiteaves); off Canso, N.S. (Cornish); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Puget Sound, Washington; Hudson Strait to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; Shetland Island; North Norway; Spitsbergen; Barents Sea; White Sea; Sea of Okhotsk.

Bathymetric range: 0–285 m.

Genus *Posterula* Jullien and Calvet, 1903

Posterula sarsii (Smitt, 1867) (Plate VI, *c*, *d*)

Eschara sarsii Busk, 1878, p. 287; 1880, p. 237.

Escharoides sarsi Hincks, 1888, p. 218, pl. 14, fig. 1; Whiteaves, 1901, p. 102.

Posterula sarsi Jullien and Calvet, 1903, p. 89, pl. 11, fig. 4.

Escharopsis sarsi Nordgaard, 1906, p. 26; Osburn, 1912, p. 286.

Posterula sarsi Osburn, 1936, p. 541; Hansen, 1962, p. 30.

Escharopsis sarsi Kluge, 1962, p. 547, text-fig. 384.

Material examined. — stations 103, 126, 232, 322, 333, 334, 811, 61-2, 61-32, 61-43, 65-1506.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk); Northwest Baffin Bay (Nordgaard, Osburn, Hansen); Fury and Hecla Strait, off Cape Sable, N.S. (Osburn); Labrador (Osburn, Kluge); Newfoundland (Jullien and Calvet); Gulf of St. Lawrence (Hincks, Whiteaves). (*b*) *Coastal North America*: Point Barrow to Juneau, Gulf of Alaska; Franklin Pierce Bay, Kane Basin to Mount Desert Island, Gulf of Maine. (*c*) *Elsewhere*: West and East Greenland; Iceland;

Jan Mayen Island; North Norway; Barents Sea; Spitsbergen; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 4–1267 m.

Family SCHIZOPORELLIDAE

Genus *Schizoporella* Hincks, 1877b

Schizoporella obesa (Waters, 1900) (Plate VII, *b*)

Hippodiplosia obesa Kluge, 1962, p. 498, text-fig. 344.

Material examined. — stations 106, 126, 206, 549, 65-1505, 65-1506.

Remarks. — This is a problematical species. Its placement in the genus *Hippodiplosia* (Kluge, 1962) (=*Hippoporina*), however, has no sound morphological basis. I have assigned it here to the genus *Schizoporella* instead.

Distribution. — The *Calanus* material comprises only the second record for the species in the Canadian area, the first being that of Kluge (1962) from the Gulf of St. Lawrence. *Elsewhere*: Barents Sea; White Sea; Kara Sea; Sea of Okhotsk; Bering Sea; Sea of Japan.

Bathymetric range: 24–450 m.

Schizoporella stylifera (Levinsen, 1886) (Plate VII, *a*)

The following references pertain to arctic North America:

Schizoporella condylata Nordgaard, 1906, p. 18, pl. 2, fig. 16–18.

Emballotheca stylifera Osburn, 1953, p. 777, pl. 81, fig. 5.

Schizoporella stylifera; also var. *perforata* Kluge, 1962, p. 489, 490, text-fig. 335, 336.

Material examined. — station 61-32.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Kluge). (*b*) *Coastal North America*: Point Barrow, Alaska (Osburn); Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Barents Sea; Kara Sea; Laptev Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 42–252 m.

Genus *Schizomavella* Canu and Bassler, 1917

Schizomavella auriculata (Hassall, 1842)

Lepralia globifera Packard, 1863, p. 408; 1867, p. 271.

Schizoporella auriculata Whiteaves, 1901, p. 100.

Schizoporella lineata Nordgaard, 1906, p. 16; Osburn, 1912, p. 280.

Schizomavicella (sic) *auriculata* Osburn, 1923, p. 9D.

Schizomavella (*Schizoporella*) *auriculata* Osburn, 1932, p. 31.

Schizomavella auriculata Hansen, 1962, p. 31; Powell, 1968.

Material examined. — stations 58-21, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Dolphin and Union Strait, Hudson Strait, Newfoundland (Osburn); Labrador (Kluge); Belle Isle Strait (Packard); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Prince Rupert, B.C. to southern California; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West Greenland; Iceland; British Isles; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–1285 m.

Schizomavella porifera (Smitt, 1867)

Not *Smittia landsborovii* form *porifera* Hincks, 1888, p. 225, pl. 14, fig. 2 (=*Smittina majuscula* (Smitt) q.v.).

Codonellina operculata Mawatari, 1956, p. 125, fig. 8*h–k*; 9*c*.
Schizomavella porifera Powell, 1968.
Material examined. — stations 33, 229, 232, 333, 65-1510.

Remarks. — Mawatari's description and figures indicate *Codonellina operculata* from the Kurile Islands to be a synonym of the present species.

Distribution. — (*a*) *Coastal North America*: Point Barrow, Alaska; Gulf of St. Lawrence to the Bay of Fundy. (*b*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; Sea of Okhotsk; Bering Sea; Sea of Japan.
Bathymetric range: 0–360 m.

Genus *Stephanosella* Canu and Bassler, 1917
Stephanosella biaperta (Michelin, 1845)

Schizoporella biaperta Whiteaves, 1901, p. 100; Nordgaard, 1906, p. 15, pl. 1, fig. 12–14.
Material examined. — stations 126, 334, 65-1506.
Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Point Barrow Alaska; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West Greenland; Jan Mayen Island; Spitsbergen; Barents Sea; White Sea· Kara Sea; Laptev Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.
Bathymetric range: 18–256 m.

Family MICROPORELLIDAE
Genus *Microporella* Hincks, 1877b
Microporella ciliata (Pallas, 1766)

Microporella ciliata Whiteaves, 1901, p. 98; Osburn, 1912, p. 279; 1923, p. 10D; 1932, p. 13
Microporella ciliata var. *arctica* Kluge, 1962, p. 519, text-fig. 362.
Microporella ciliata Powell and Crowell, 1967, p. 342.
Material examined. — stations 126, 707.
Distribution. — (*a*) *Canadian*: Dolphin and Union Strait, Hudson Strait (Osburn); Labrador (Osburn); Gulf of St. Lawrence (Whiteaves, Kluge); Bay of Fundy (Powell and Crowell). (*b*) *Elsewhere*: widely distributed in arctic, temperate, and tropical seas.
Bathymetric range: 0–570 m.

Family HIPPORORINIDAE
Genus *Hippoporina* Neviani, 1895
Hippoporina cancellata (Smitt, 1867) (Plate VII, *d*)

Smittina cancellata Nordgaard, 1906, p. 29.
Material examined. — stations 30, 33.
Distribution. — Nordgaard (1906) mentioned this species in his monograph but as he pointed out it was not among the material obtained by the second Norwegian Arctic Expedition (1898–1902). The *Calanus* specimens, therefore, constitute the first record for the species in the Canadian area. *Elsewhere*: Beaufort Sea (Osburn, 1953); Spitsbergen (Smitt); Barents Sea (Kluge, 1962).
Bathymetric range: 18–134 m.

Hippoporina propinqua (Smitt, 1867)

Hippoporina propinqua Powell, 1968 (references).
Material examined. — stations 33, 58, 103, 126, 201C, 225, 226, 406, 522, 553, 818, 821, 59-29, 61-10, 61-26, 61-43.

Distribution. — (*a*) *Canadian*: Labrador (Hincks, 1877a); off Cape Sable, N.S. (Osburn, 1912); Bay of Fundy (Powell). (*b*) *Coastal North America*: Frobisher Bay to Cape Cod, Massachusetts; not recorded from the western American arctic or eastern Pacific. (*c*) *Elsewhere*: West and East Greenland; Iceland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Bering Sea; Sea of Okhotsk.

Bathymetric range: 1–210 m.

Hippoporina reticulatopunctata (Hincks, 1877a) (Plate VII, *c*)

Smittia reticulatopunctata Whiteaves, 1901, p. 107.

"Lepralia" reticulato-punctata Norman, 1903b, p. 122.

Schizoporella reticulato-punctata Nordgaard, 1906, p. 17.

Smittia reticulatopunctata Osburn, 1912, p. 286.

Hippoporina reticulatopunctata Powell, 1968.

Material examined. — stations 7, 33, 58, 126, 201C, 317, 547, 61-26, 62-2031.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves, Norman); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Icy Cape, Alaska; Jones Sound, Baffin Bay to Cape Anne, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–306 m.

Family CELLEPORINIDAE

Genus *Celleporina* Gray, 1848

Celleporina surcularis (Packard) (Plate VIII, *a*, *b*)

Celleporaria surcularis Packard, 1863, p. 410; 1867, p. 274.

Porella surcularis Whiteaves, 1901, p. 104.

Cellepora incrassata Nordgaard, 1906, p. 35.

Cellepora surcularis Osburn, 1912, p. 281.

Schizomopora (*Cellepora*) *surcularis* Osburn, 1923, p. 12D.

Costazia (*Cellepora*) *surcularis* Osburn, 1932, p. 15; 1936, p. 542.

Celleporina surcularis Hansen, 1962, p. 48.

Material examined. — stations 103, 107, 208, 210, 221, 226, 229, 317, 318, 319, 322, 331, 333, 334, 406, 542, 547, 549, 610, 616, 815, 818, 61-1, 61-18, 61-24, 61-30, 61-32, 61-40, 61-43, 65-1506, 65-1510.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Fury and Hecla Strait, Hudson Strait, Labrador, Newfoundland, off Cape Sable, N.S. (Osburn); Belle Isle Strait (Packard); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Point Barrow, Alaska to northern California (Robertson, 1908, p. 313); Jones Sound, Baffin Bay to Cape Sable, N.S. (*c*) *Elsewhere*: West Greenland; Iceland; Faeroes; North Norway; Spitsbergen; Barents Sea; White Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–450 m.

Celleporina ventricosa (Lorenz, 1886) (Plate VIII, *c*, *d*)

Cellepora ventricosa Nordgaard, 1906, p. 35.

Costazia (*Cellepora*) *ventricosa* Osburn, 1932, p. 16; 1936, p. 542.

Celleporina ventricosa Hansen, 1962, p. 49.

Cellepora ventricosa Kluge, 1962, p. 554, text-fig. 389.

Material examined. — stations 28, 103, 106, 107, 206, 210, 226, 332, 333, 334, 547, 616, 61-8, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Fury and Hecla Strait, Foxe Basin, Hudson Strait (Osburn); Gulf of St. Lawrence (Kluge). (*b*) *Coastal North America*: Point Barrow, Alaska to Dillon Beach, northern California; Jones Sound, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Iceland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Sea of Okhotsk; Kurile Islands.

Bathymetric range: 12–460 m.

Genus *Schismopora* MacGillivray, 1888

Schismopora nodulosa (Lorenz, 1886) (Plate IX, *a*, *b*)

Material examined. — stations 103, 333, 547, 811.

Distribution. — Not previously known from the Canadian arctic; Fury and Hecla Strait (*Calanus* Station 811) comprises the most western range recorded to date for the species. As *S. nodulosa* has not been taken from the Chukchi and Beaufort seas, it may have an Atlantic–arctic range. *Elsewhere*: East Greenland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea.

Bathymetric range: 1–698 m.

Family ESCHARELLIDAE

Genus *Escharella* Gray, 1848

Escharella immersa (Fleming, 1828)

Mucronella peachii Whiteaves, 1901, p. 107.

Escharella immersa Powell and Crowell, 1967, p. 342; Powell, 1968.

Material examined. — stations 106, 206, 208.

N.M.C. Cat. No. 254; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell and Crowell). (*b*) *Coastal North America*: Hudson Strait to Long Island Sound, Connecticut; not known in the western American arctic or eastern Pacific. (*c*) *Elsewhere*: West and East Greenland; Faeroes; Jan Mayen Island: British Isles; North Sea; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; East Siberian Sea; Bering Sea; Sea of Okhotsk.

Bathymetric range: 0–1331 m.

Escharella abyssicola (Norman, 1868)

Mucronella abyssicola Whiteaves, 1901, p. 107.

Escharella abyssicola Nordgaard, 1906, p. 27.

Material examined. — stations 106, 208, 58-21.

Distribution. — Atlantic–arctic; not occurring in the far eastern Soviet and western American arctic areas. (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Faeroes; Jan Mayen Island; Shetland Islands; West Norway; Spitsbergen; Barents Sea.

Bathymetric range: 5–500 m.

Escharella connectens (Ridley, 1881) (Plate X, *a*)

Mucronella (*Escharella*) *indivisa* Osburn, 1923, p. 10D.

Mucronella indivisa Osburn, 1932, p. 14.

Mucronella connectens Osburn, 1936, p. 542.

Material examined. — stations 221, 232, 547.

Distribution. — Both Hansen (1962, p. 66) and Kluge (1962, p. 407) consider this to be a high-arctic species. (*a*) *Canadian*: northwest Baffin Bay, Dolphin and Union Strait, Fury and

Hecla Strait, Frozen Strait, Hudson Strait (Osburn). (*b*) *Coastal North America*: Point Barrow, Alaska; Coburg Island, Baffin Bay to Hudson Strait. (*c*) *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea.

Bathymetric range: 1–300 m.

Escharella thompsoni (Kluge, 1955) (Plate IX, *d*)

Smittina thompsoni Kluge, 1962, p. 439, text-fig. 291.

Material examined. — stations 106, 65-1506.

Description (*translated from the Russian*; *Kluge, 1962, p. 439–440*). — "Zoarium encrusting, zooids arranged in regular or irregular rows. Zooids of average size (length 0.65–0.88 mm, width 0.63–0.75 mm) irregularly hexagonal or rhomboidal, broad, thick walled with irregularly depressed margins. Frontal surface moderately convex, granular, the marginal depressions extended radially. A small round pore is situated at the base of each depression. A large broad frontal tubercle is often formed as a result of progressive calcification and thickening of the frontal wall. Primary orifice rounded, situated at the distal extremity of the zooid, the proximal margin forming a broad lyrula which extends steeply downwards, broadening towards its free margin and forming sharp angles, directed transversely. Distal portion of the secondary orifice semicircular, the proximal portion narrowing into a short sinus. A small avicularium with a semicircular mandible is positioned within the sinus of the secondary orifice. The avicularian chamber situated beneath the frontal surface may be located on either side of the sinus, depending on the orientation of the mandible. Ovicells entozooecial, protruding slightly at the surface.

"Lives on shell and rock at a depth of 80–162 m.

Distribution. — "I discovered this species at Disko Island, Baffin Bay."

Remarks. — The well-developed lyrula together with the marginally perforated frontal wall and the imperforate ovicell are characters diagnostic of the genus *Escharella* to which this species is referred here. It should be noted, however, that the inter-oral type of avicularium in Kluge's species is a feature not usually associated with *Escharella*.

Escharella thompsoni was originally taken from West Greenland (Kluge, 1955). The *Calanus* material constitutes the only subsequent record, the first for the eastern Canadian subarctic.

Escharella ventricosa (Hassall, 1842) (Plate IX, *c*)

Lepralia crassispina Packard, 1863, p. 406.

Mucronella ventricosa Whiteaves, 1901, p. 107.

Escharella ventricosa Nordgaard, 1906, p. 27.

Mucronella ventricosa Osburn, 1912, p. 283; 1923, p. 10D; 1932, p. 14.

Escharella ventricosa Powell, 1968.

Material examined. — stations 20, 21, 33, 103, 106, 126, 413, 616, 723, 901, 61-1015, 65-1506. N.M.C. Cat. No. 254; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Hudson Strait, Labrador (Osburn); Belle Isle Strait (Packard); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to the Oregon Coast; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Faeroes; British Isles; West Norway; Kattegat; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chuckhi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–1262 m.

Family SMITTINIDAE
Genus *Smittina* Norman, 1903b
Smittina bella (Busk, 1860)

Lepralia producta Packard, 1863, p. 407, pl. 2, fig. 1 (part q. v.).
Porella bella Norman, 1894, p. 125; Whiteaves, 1901, p. 103.
Smittina bella Nordgaard, 1918, p. 67; Powell, 1968.
Material examined. — station 65-1506.

Remarks. — As stated previously, the material Packard (1863, p. 407) described and illustrated as a juvenile stage of *Lepralia producta* is referable to the present species instead.

Smittina bella and *S. rigida* (Lorenz q.v.) bear rather close resemblances; both have a pyriform secondary orifice and a heavily calcified frontal wall, also a median pore on the frontal surface of the ovicell. The former species is primarily distinguished by the oval-shaped inter-oral avicularium (spatulate in *S. rigida*), and the smaller lyrula (see Mawatari, 1956, p. 131, text-fig. 12*c*).

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Norman, Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Icy Cape, Alaska; Jones Sound, Baffin Bay to Mount Desert Island, Maine. (*c*) *Elsewhere*: West and East Greenland; Iceland; British Isles; West Norway; Spitsbergen; Sea of Okhotsk; Kurile Islands.
Bathymetric range: 0–100 m.

Smittina groenlandica (Norman, 1893)

Schizoporella bidenkapi Nordgaard, 1906, p. 19, pl. 2, fig. 22–24.
Porella groenlandica Kluge, 1962, p. 456, text-fig. 303.
Material examined. — stations 126, 208, 210, 333, 65-1506.

Remarks. — Although a lyrula is wanting, the perforate frontal wall and immersed inter-oral avicularium provide strong evidence for referring this species to the genus *Smittina*.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Kluge). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to the Gulf of St. Lawrence; not known from the western American arctic or northern Pacific. (*c*) *Elsewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk.
Bathymetric range: 14–280 m.

Smittina majuscula (Smitt, 1867)

Smittina arctica Osburn, 1936, p. 542; 1952, p. 402, text-fig. 13, 14.
Smittina majuscula Powell, 1968 (references).
Material examined. — stations 28, 33, 102, 333, 413, 62-009.
Distribution. — (*a*) *Canadian*: northwest Baffin Bay, Hudson Bay (Osburn); Gulf of St. Lawrence (Hincks, 1888; Whiteaves, 1901); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska; Coburg Island, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Eisewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Bering Sea; Sea of Japan.
Bathymetric range: 0–327 m.

Smittina mucronata (Smitt, 1867) (Plate X, *b*)

Material examined. — stations 33, 231.

Distribution. — The *Calanus* material comprises the first record of this species in the Canadian area, representing also its westernmost range recorded to date. *Elsewhere*: North Norway; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 9–252 m.

Smittina rigida (Lorenz, 1886) (Plate X, *c*)

Smittina novanglia Osburn, 1933, p. 50, pl. 9, fig. 8, 9; pl. 13, fig. 7, 8; pl. 14, fig. 5.

Material examined. — stations 103, 126, 210, 334, 616, 58-21, 65-1506.

Distribution. — Thus far, this species has not been taken from the western American arctic or the eastern Pacific. (*a*) *North America*: Mt. Desert Island, Georges Bank (Gulf of Maine); Nantucket Island, Massachusetts (Osburn). (*b*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Shetland Islands; West Norway; Barents Sea; White Sea; Kara Sea; Laptev Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 14–250 m.

Genus *Cystisella* Canu and Bassler, 1917

Cystisella saccata (Busk, 1856) (Plate XI, *a*, *b*)

Eschara elegantula Packard, 1863, p. 411; 1867, p. 275; Busk, 1878, p. 286; 1880, p. 235; 1884, p. 141, pl. 20, fig. 6 (not of d'Orbigny).

Porella elegantula Hincks, 1888, p. 222, pl. 15, fig. 5; Whiteaves, 1901, p. 104 (not of d'Orbigny).

Porella saccata Nordgaard, 1906, p. 23, pl. 3, fig. 38; Osburn, 1912, p. 283, pl. 34, fig. 4.

Cysticella (sic) *saccata* Osburn, 1923, p. 11D.

Cystisella (*Porella*) *saccata* Osburn, 1932, p. 15; 1936, p. 542.

Cystisella saccata Hansen, 1962, p. 43.

Porella saccata Kluge, 1962, p. 462, text-fig. 309.

Material examined. — stations 13, 20, 21, 30, 33, 58, 201C, 221, 226, 322, 333, 334, 406, 520, 808, 811, 815, 818, 820, 837, 901, 58-28, 58-33, 59-21, 59-46, 59-58, 59-69, 61-10, 61-11, 61-26, 62-009, 62-2012, 62-2014, 62-2032, 65-1506, 65-1510.

N.M.C. Cat. No. 256; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Remarks. — This is one of the dominant species in the collections, colonies being readily distinguishable by the flattened, bilaminate growth habit of the branches (Plate XI, *b*).

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk, 1880); northwest Baffin Bay (Osburn, Hansen); Dolphin and Union Strait, Hudson Bay, Hudson Strait, Newfoundland (Osburn); Labrador (Osburn, Kluge); Strait of Belle Isle (Packard); Gulf of St. Lawrence (Hincks, Whiteaves); off Nova Scotia (Busk, 1884). (*b*) *Coastal North America*: Point Barrow, Icy Cape, Alaska; Cape Napoleon, Kane Basin to Nova Scotia (off the southern coast). (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Iceland; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 1–332 m.

Cystisella elegantula (d'Orbigny, 1851) (Plate XI, *c*, *d*)

Eschara elegantula d'Orbigny 1851, p. 102.

Not *Eschara elegantula* Packard, 1863, p. 411; 1867, p. 275. (= *Cystisella saccata* (Busk) q.v.).

Eschara perpusilla Busk, 1878, p. 287; 1880, p. 236, pl. 13, fig. 5.
Porella perpusilla Osburn, 1912, p. 284, pl. 34, fig. 5, *a*, *b*.
Cystisella (*Porella*) *elegantula* Osburn, 1932, p. 15.
Cystisella elegantula Hansen, 1962, p. 42.
Material examined. — stations 33, 49, 226, 406, 61-8, 61-26.

Remarks. — The low, bushy cylindrical type of growth habit, also the gigantic lateral avicularia (Plate XI, *c*) readily distinguish this species from *C. saccata* (Busk).

Distribution. — The range of this species extends only over 40° of longitude, i.e. between 50 and 90°W (Fig. 7). (*a*) *Canadian*: North Baffin Bay (Busk); northwest Baffin Bay (Hansen); Hudson Strait, Labrador (Osburn); Strait of Belle Isle (Packard); Newfoundland (d'Orbigny). (*b*) *Coastal North America*: Franklin Pierce Bay; Kane Basin to the Grand Banks, Newfoundland. (*c*) *Elsewhere*: West Greenland (Levinsen, 1916).
Bathymetric range: 0–150 m.

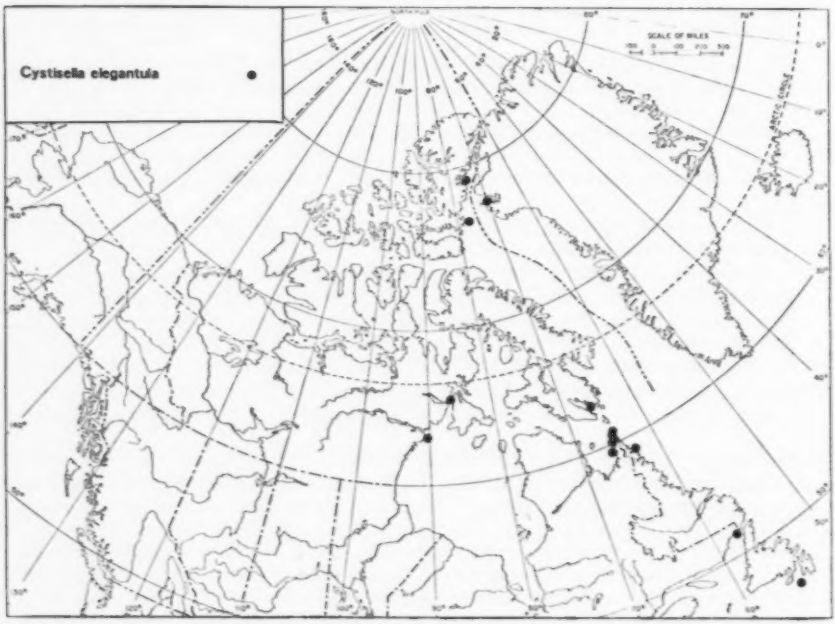

FIG. 7. Total distribution of *Cystisella elegantula*.

Genus *Parasmittina* Osburn, 1952
Parasmittina jeffreysi (Norman, 1876) (Plate X, *d*)

Smittina jeffreysi Norman, 1903b, p. 120; Nordgaard, 1906, p. 28, pl. 4, fig. 48.
Smittina jefftreysi (sic) Kluge, 1962, p. 438, text-fig. 290.
Parasmittina jeffreysi Powell, 1968.
Material examined. — stations 20, 21, 226, 334, 715, 722, 811, 58-21, 59-21, 61-30, 61-32, 61-43, 62-2012, 62-2014, 62-2032, 65-1044, 65-1048, 65-1506, 65-1510.

N.M.C. Cat. No. 255; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.
N.M.C. Cat. No. 258; June 2, 1963; 48°45′N, 53°13′W, 183 m.

Remarks. — The massive tubular growth habit usually associated with colonies of *P. jeffreysi*, particularly in the northern area of its range (colonies in the southern part, e.g. Bay of Fundy, are of the encrusting type) is exhibited by all of the present material.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Labrador (Kluge); Gulf of St. Lawrence (Norman); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to Mount Desert Island, Gulf of Maine. (*c*) *Elsewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 5–400 m.

Genus *Porella* Gray, 1848

Porella compressa (Sowerby, 1806) (Plate XII, *a*)

Porella compressa Osburn, 1923, p. 11D; 1932, p. 15; 1936, p. 542; Hansen, 1962, p. 34; Kluge, 1962, p. 450, text-fig. 297.

Material examined. — stations 106, 210, 231, 232, 333, 334, 815, 61-1, 61-5, 61-8, 65-1502, 65-1506, 65-1510.

N.M.C. Cat. No. 252; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Hansen); Fury and Hecla Strait, Hudson Bay, Hudson Strait (Osburn); Labrador (Hansen, Kluge). (*b*) *Coastal North America*: Point Barrow, Alaska; Clarence Head, Baffin Bay to Labrador (off Hamilton Inlet). (*c*) *Elsewhere*: West and East Greenland; Iceland; Faeroes; Jan Mayen Island; British Isles; West Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–323 m.

Porella acutirostris Smitt, 1867

Porella acutirostris Hincks, 1889, p. 429, pl. 21, fig. 5; Whiteaves, 1901, p. 103; Nordgaard, 1906, p. 24; Osburn, 1923, p. 11D; 1932, p. 15; 1936, p. 542; Powell, 1968.

Material examined. — stations 20, 21, 28, 102, 901, 61-26.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Fury and Hecla Strait, Hudson Strait (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Santa Barbara Island, southern California; Jones Sound, Baffin Bay to Long Island Sound, Connecticut. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; North Norway; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–395 m.

Porella aperta (Boeck, 1862) (Plate XII, *d*)

Porella aperta Norman, 1903b, p. 113.

Smittina (*Porella*) *laevis* Osburn, 1923, p. 10D.

Material examined. — stations 62-2031, 62-2032.

Distribution. — Atlantic-arctic; not occurring in the far eastern Soviet and western American arctic regions. (*a*) *Canadian* (Fig. 8): Dolphin and Union Strait (Osburn); Gulf of St. Lawrence (Norman). (*b*) *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea.

Bathymetric range: 19–160 m.

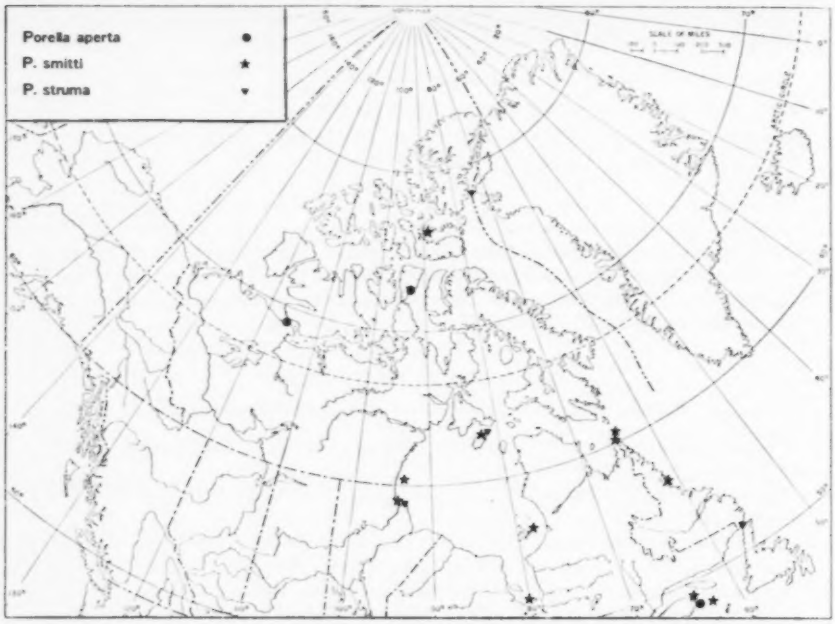

FIG. 8. Canadian distribution of *Porella aperta*, *P. smitti*, and *P. struma*.

Porella concinna (Busk, 1852)

Porella concinna Hincks, 1889, p. 428, pl. 21, fig. 4; Whiteaves, 1901, p. 102; Nordgaard, 1906, p. 24; Cornish, 1907, p. 78; Osburn, 1912, p. 283; 1923, p. 10D; 1932, p. 14; Hansen, 1962, p. 36; Powell, 1968.

Material examined. — stations 33, 229, 61-1, 65-1505, 65-1506.

N.M.C. Cat. No. 259; June 2, 1963; 48°45′N, 53°13′W, 183 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen); Hudson Strait, Labrador, Newfoundland, off Cape Sable, N.S. (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves); off Canso, N.S. (Cornish); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to San Pedro, southern California; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Faeroes; British Isles; North Sea; West Norway; Skagerrak; Kattegat; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–1165 m.

Porella minuta Norman, 1868

Porella alba Nordgaard, 1906, p. 25, pl. 3, fig. 43–46.

Porella minuta Powell and Crowell, 1967, p. 343, pl. 3, fig. 9 (references).

Material examined. — stations 126, 203, 317.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell and Crowell). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to the Bay of Fundy. (*c*) *Elsewhere*: British Isles; North Norway; Spitsbergen; Barents Sea; White Sea; Bering Sea.

Bathymetric range: 0–55 m.

Porella smitti Kluge, 1907

Porella proboscidea Nordgaard, 1906, p. 25; Osburn, 1912, p. 285; 1932, p. 15. (not of Hincks, 1888).

Porella smitti Powell, 1968 (further references).

Material examined. — stations 103, 225, 226, 611, 59-2, 59-21, 61-1.

Distribution. — (*a*) *Canadian* (*Fig. 8*): northwest Baffin Bay (Nordgaard); Hudson Bay, Labrador, off Cape Sable, N.S. (Osburn); Gulf of St. Lawrence (Whiteaves, 1901, p. 103); Bay of Fundy (Powell). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to Nantucket Island, Massachusetts; not known from the western American arctic or the eastern Pacific. (*c*) *Elsewhere*: West Greenland; Iceland; North Sea; North Norway; Barents Sea; White Sea; Kara Sea; Sea of Okhotsk.

Bathymetric range: 9–293 m.

Porella struma (Norman, 1868) (Plate XII, *b*)

Porella struma Whiteaves, 1901, p. 103; Norman, 1903b, p. 113; Osburn, 1912, p. 285; 1932, p. 15; Kluge, 1962, p. 451, text-fig. 298; Hansen, 1962, p. 34.

Material examined. — stations 613, 65-1510.

Distribution. — Atlantic–arctic; not known from the far eastern Soviet and western American arctic areas. (*a*) *Canadian* (*Fig. 8*): North Baffin Bay (Hansen); Hudson Bay (Osburn); Labrador (Kluge); Gulf of St. Lawrence (Whiteaves, Norman); off Cape Sable, N.S. (Osburn). (*b*) *Coastal North America*: Smith Sound, Baffin Bay to Nova Scotia (off the south coast). (*c*) *Elsewhere*: West Greenland; Iceland; Shetland Islands; West Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea.

Bathymetric range: 6–672 m.

Genus *Pseudoflustra* Bidenkap, 1897

Remarks. — This is an indigenous panarctic genus, comprising five species, viz. *P. solida* (Stimpson), *P. sinuosa* (Andersson), *P. anderssoni* Kluge, *P. birulai* Kluge, and *P. hincksi* Kluge. According to distributional data (Kluge, 1962), all five are confined to the Atlantic–arctic faunal province.

Pseudoflustra solida (Stimpson, 1853) (Plate XII, *c*)

Flustra solida Stimpson, 1853, p. 19, fig. 12; Hincks, 1892, p. 149, pl. 8, fig. 1; Whiteaves, 1901, p. 95.

Smittina solida Osburn, 1923, p. 10D.

Pseudoflustra solida Osburn, 1932, p. 14.

Material examined. — stations 59-66, 61-35, 62-2014, 62-2031, 62-2032, 65-1044, 65-1048.

N.M.C. Cat. No. 148; June 3, 1963; 48°13′N, 50°05′W, 183 m.

N.M.C. Cat. No. 237; July 27, 1952; Prince Patrick Island, 30–45 m.

N.M.C. Cat. No. 244; August 19, 1954; Ellef Ringnes Island, 46 m.

Distribution. — Atlantic–arctic; Prince Patrick Island (120°W long) comprising the western-most range for the species. According to recent data (Kluge, 1962, p. 442), *P. solida* has not been taken from the Chukchi, Bering, or Beaufort seas, hence its distribution is not circumpolar as is sometimes postulated (Nordgaard, 1929, p. 7; Hansen, 1962, p. 37). (*a*) *Canadian* (*Fig. 9*): Dolphin and Union Strait, Hudson Bay (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves); Bay of Fundy (Stimpson). (*b*) *Coastal North America*: Isachsen, Ellef Ringnes Island to Dolphin and Union Strait; Hudson Bay to Cashes Ledge, Gulf of Maine. (*c*) *Further distribution*: West and East Greenland; Iceland; Jan Mayen Island; West Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea.

Bathymetric range: 4–1275 m.

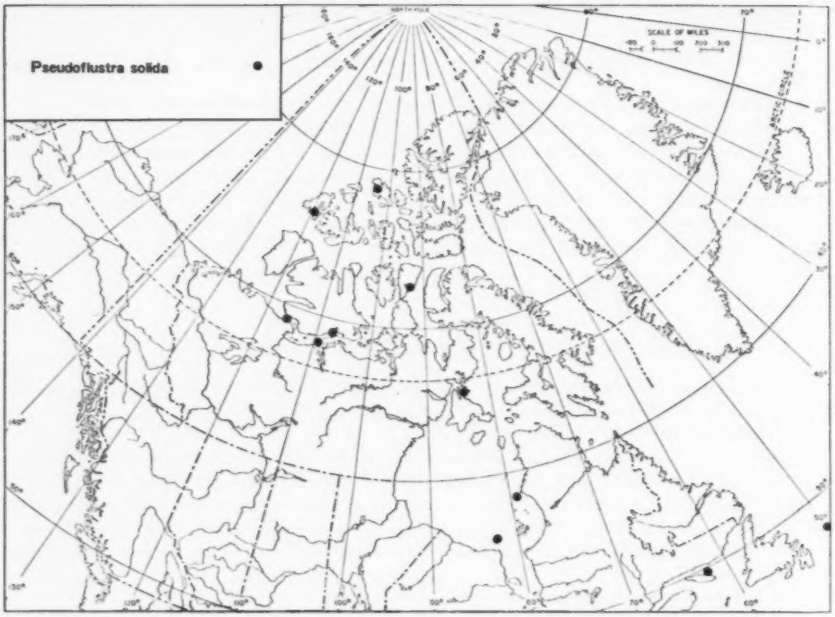

FIG. 9. Canadian distribution of *Pseudoflustra solida*.

Pseudoflustra sinuosa (Andersson, 1902)

Material examined. — N.M.C. Cat. No. 147; June 3, 1963; 48°13′N, 50°05′W, 183 m.

Remarks. — The *A. T. Cameron* material constitutes the first record for this "high arctic bathy-pelagic species" (Kluge, 1962, p. 446) in the Canadian area.

Distribution. — East Greenland; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea.
Bathymetric range: 1–1000 m.

Genus *Rhamphostomella* Lorenz, 1886

Rhamphostomella costata Lorenz, 1886

Rhamphostomella costata Hincks, 1889, p. 426, pl. 21, fig. 6–8; Whiteaves, 1901, p. 108; Nordgaard, 1906, p. 30; Osburn, 1912, p. 286; 1932, p. 14; 1936, p. 542; Hansen, 1962, p. 41; Powell, 1968.

Material examined. — stations 58, 203, 226, 232, 318, 553, 61-26, 61-39, 62-2031, 65-1502. N.M.C. Cat. No. 238; July 27, 1952; Prince Patrick Island, 30–45 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Labrador, Hudson Strait, off Cape Sable, N.S. (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Mould Bay, Prince Patrick Island to Puget Sound, Washington; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.
Bathymetric range: 0–360 m.

Rhamphostomella bilaminata (Hincks, 1877a)

Cellepora bilaminata Hincks, 1877a, p. 111, pl. 11, fig. 6, 7.

Rhamphostomella bilaminata Hincks, 1889, p. 426; Whiteaves, 1901, p. 108; Nordgaard, 1906, p. 33, pl. 4, fig. 57; Osburn, 1932, p. 14; 1936, p. 542; Powell, 1968.

Material examined. — stations 33, 58, 201C, 203, 226, 65-1502.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn); Hudson Strait (Osburn); Labrador (Hincks); Gulf of St. Lawrence (Hincks, Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Icy Cape, Alaska to Cape Ebenshaw, B.C., Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Jan Mayen Island; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–226 m.

Rhamphostomella hincksi Nordgaard, 1906 (Plate XIII, *a*)

Ramphostomella (sic) *hincksi* Nordgaard, 1906, p. 31, pl. 4, fig. 51.

Rhamphostomella hincksi Hansen, 1962, p. 40.

Material examined. — stations 126, 229, 318, 406, 723, 62-2032.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Hansen). (*b*) *Coastal North America* (*Fig. 10*): Point Barrow to Pavlof Bay, Alaska; Clarence Head, Baffin Bay to Hudson Strait. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; Barents Sea; Kara Sea; Laptev Sea; Chukchi Sea; Sea of Okhotsk; Kurile Islands.

Bathymetric range: 4–270 m.

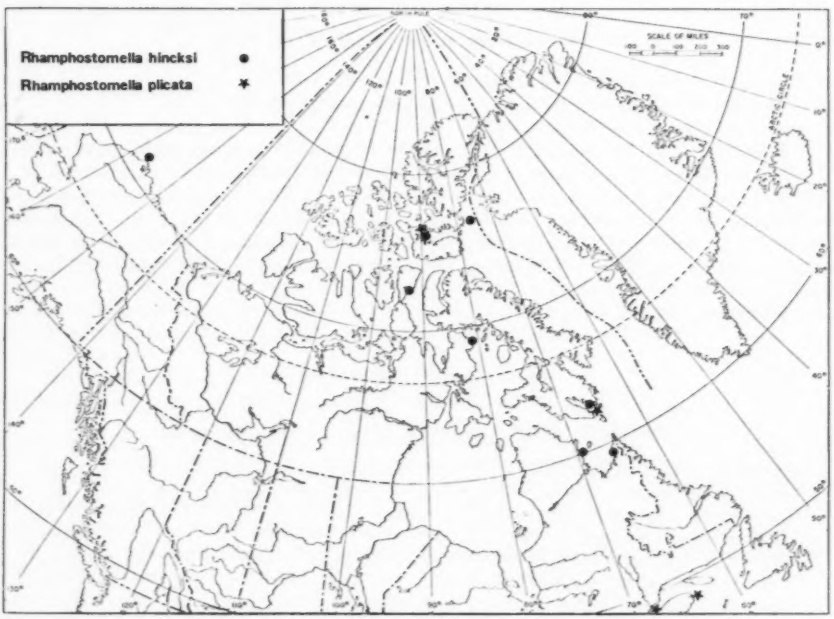

FIG. 10. North American distribution of *Rhamphostomella hincksi* and *R. plicata*.

Rhamphostomella ovata (Smitt, 1867)

Cellepora ovata Hincks, 1877a, p. 112.

Rhamphostomella ovata Whiteaves, 1901, p. 108; Nordgaard, 1906, p. 32; Osburn, 1912, p. 286; 1932, p. 14; 1936, p. 542; Powell and Crowell, 1967, p. 343; Powell, 1968.

Material examined. — station 33.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Fury and Hecla Strait, Frozen Strait, Hudson Bay, Hudson Strait (Osburn); Labrador (Hincks, Osburn); Gulf of St. Lawrence (Whiteaves); off Cape Sable, N.S. (Osburn); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska to Olga Bay, Gulf of Alaska; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; Faeroes; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 4–180 m.

Rhamphostomella plicata (Smitt, 1867) (Plate XIII, *b*)

Rhamphostomella plicata Hincks, 1889, p. 426; Whiteaves, 1901, p. 108; Nordgaard, 1906, p. 30, pl. 4, fig. 49, 50.

Material examined. — station 319.

Distribution. — (*a*) *Canadian* (*Fig. 10*): northwest Baffin Bay (Nordgaard); Gulf of St. Lawrence (Hincks, Whiteaves). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to the Gulf of St. Lawrence; not known from the western American arctic or eastern Pacific. (*c*) *Elsewhere*: West and East Greenland; Iceland; Faeroes; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk.

Bathymetric range: 12–132 m.

Rhamphostomella scabra (Fabricius, 1780)

Cellepora scabra Hincks, 1877a, p. 110.

Rhamphostomella scabra Whiteaves, 1901, p. 108; Nordgaard, 1906, p. 30.

Material examined. — station 62-2032.

N.M.C. Cat. No. 253; August 4, 1939, Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Labrador (Hincks) Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to Georges Bank, Gulf of Maine; I have been unable to verify the basis for Hansen's (1962, p. 41) statement "in the Pacific distributed to Puget Sound." (*c*) *Elsewhere*: West and East Greenland; North Norway; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–460 m.

Family CHEILOPORINIDAE

Genus *Cheilopora* Levinsen, 1909

Cheilopora sincera (Smitt, 1867) (Plate XIII, *d*)

Hemeschara sincera Busk, 1878, p. 287; 1880, p. 237.

Mucronella praelucida Hincks, 1888, p. 225, pl. 15, fig. 3; Whiteaves, 1901, p. 107.

"*Mucronella*" *sincera* Norman, 1903b, p. 118.

Eschara sincera Nordgaard, 1906, p. 23.

Mucronella praelucida Osburn, 1912, p. 283, pl. 34, fig. 3, *a*, *c*.

Cheilopora sincera Osburn, 1923, p. 11D.

Cheilopora praelucida Osburn, 1923, p. 11D; 1932, p. 15.

Cheilopora sincera Osburn, 1936, p. 542; Hansen, 1962, p. 46.

Material examined. — stations 30, 33, 212, 221, 229, 322, 333, 334, 61-39, 61-43, 62-2012, 62-2032.

N.M.C. Cat. No. 236; August 27, 1952; Prince Patrick Island, 30–45 m.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk); northwest Baffin Bay (Nordgaard, Osburn, Hansen); Dolphin and Union Strait, Hudson Strait, Labrador (Osburn); Gulf of St. Lawrence (Hincks, Whiteaves, Norman). (*b*) *Coastal North America*: Mould Bay, Prince Patrick Island to southern Vancouver Island, B.C., Kane Basin, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 1–513 m.

Family RETEPORIDAE

Genus *Hippoporella* Canu, 1917

Hippoporella hippopus (Smitt, 1867)

Lepralia hippopus Whiteaves, 1901, p. 101.

Eschara hipposus (sic) Nordgaard, 1906, p. 22, pl. 3, fig. 36, 37.

Lepralia hippopus Osburn, 1912, p. 282.

Hippoporella hippopus Powell, 1968.

Material examined. — stations 103, 713, 58-3, 65-1505.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard); Labrador (Osburn); Gulf of St. Lawrence (Whiteaves); Bay of Fundy (Powell). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to Cape Cod, Massachusetts. (*c*) *Elsewhere*: West and East Greenland; British Isles; North Norway, Spitsbergen; Barents Sea; White Sea; Kara Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk; Kurile Islands; Beaufort Sea.

Bathymetric range: 6–235 m.

Genus *Lepraliella* Levinsen, 1916

Lepraliella contigua (Smitt, 1867)

Cellepora contigua Whiteaves, 1901, p. 109.

Rhamphostomella contigua Nordgaard, 1906, p. 34.

Cellepora contigua Osburn, 1912, p. 281, pl. 34, fig. 1.

Lepraliella contigua Osburn, 1923, p. 11D; 1932, p. 15; 1936, p. 542; Hansen, 1962, p. 46.

Material examined. — stations 106, 126, 208, 333, 65-1506.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Hudson Strait, off Cape Sable, N.S. (Osburn). (*b*) *Coastal North America*: Point Barrow, Alaska; Jones Sound, Baffin Bay to Cape Sable, N.S. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Chukchi Sea; Bering Sea; Sea of Okhotsk.

Bathymetric range: 10–672 m.

Genus *Phidolopora* Gabb and Horn, 1862

Phidolopora elongata (Smitt, 1867) (Plate XIII, *c*)

Retepora elongata Whiteaves, 1901, p. 109.

Retepora wallichiana Nordgaard, 1906, p. 35.

Retepora elongata Osburn, 1923, p. 9D; 1936, p. 542; Kluge, 1962, p. 527, text-fig. 368.

Material examined. — stations 221, 229, 837, 61-35, 61-39, 62-2012, 62-2014, 62-2031. N.M.C. Cat. No. 251; August 4, 1939; Mouth of Lake Harbour Fiord, Baffin Island, 55 m.

Distribution. — (*a*) *Canadian* (*Fig. 11*): northwest Baffin Bay (Nordgaard, Osburn); Dolphin and Union Strait, Fury and Hecla Strait (Osburn); Labrador (Kluge); Gulf of St. Lawrence

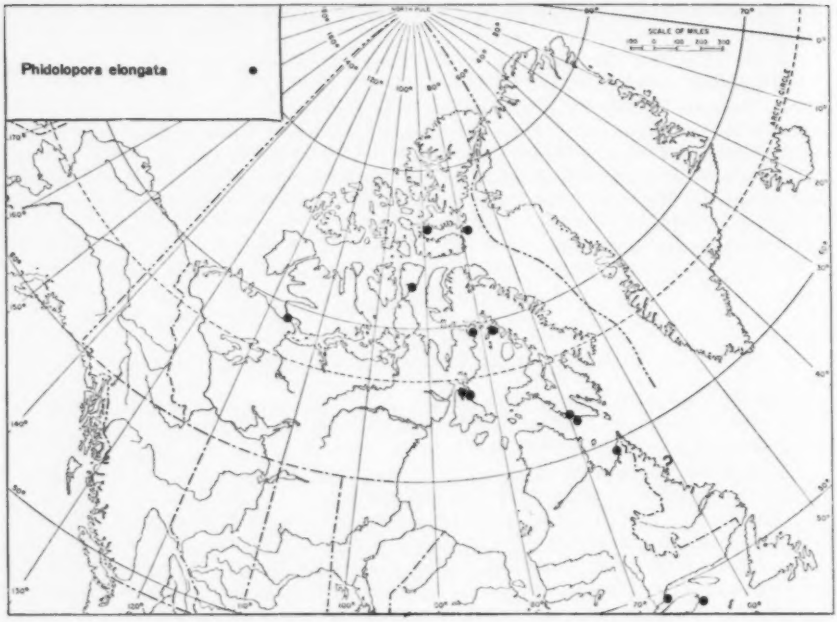

FIG. 11. Canadian distribution of *Phidolopora elongata*.

(Whiteaves). (*b*) *Coastal North America*: Jones Sound, Baffin Bay to the Gulf of St. Lawrence; not known from the western American arctic or the eastern Pacific. (*c*) *Elsewhere*: West and East Greenland; North Norway; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Bering Sea; Sea of Japan.

Bathymetric range: 1–450 m.

Family MYRIAPORIDAE
Genus *Myriapora* de Blainville, 1830
Myriapora coarctica (M. Sars, 1850) (Plate XIV, *b*)

Myriozoum coarcticum Busk, 1878, p. 286; 1880, p. 234; Whiteaves, 1901, p. 99; Osburn, 1912, p. 281; Hansen, 1962, p. 49.

Material examined. — station 106.

Distribution. — (*a*) *Canadian*: North Baffin Bay (Busk); northwest Baffin Bay (Hansen); Labrador (Osburn); off Nova Scotia (Whiteaves). (*b*) *Coastal North America*: Orca, Gulf of Alaska to Oregon; Franklin Pierce Bay, Kane Basin to La Have, N.S. (*c*) *Elsewhere*: West and East Greenland; Iceland; Jan Mayen Island; North Norway; Barents Sea; White Sea; Kara Sea; Sea of Okhotsk.

Bathymetric range: 24–428 m.

Myriapora subgracila (d'Orbigny, 1853) (Plate XIV, *c*, *d*)

Myriozoum subgracile d'Orbigny, 1853, p. 662; Packard, 1863, p. 411, pl. 2, fig. 5; 1867, p. 276; Whiteaves, 1901, p. 99; Jullien and Calvet, 1903, p. 55.

Leieschara subgracile Nordgaard, 1906, p. 15.

Myriozoum subgracile Osburn, 1932, p. 16; 1936, p. 542; Hansen, 1962, p. 49.

Leieschara subgracilis Kluge, 1962, p. 510, text-fig. 355.

Material examined. — stations 106, 210, 221, 229, 232, 610, 704, 715, 719, 722, 811, 815, 818, 59-69, 61-1, 61-13, 61-32, 62-2003, 62-2014, 65-1502, 65-1506, 65-1510.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn, Hansen); Hudson Bay (Osburn); Labrador (Kluge); Strait of Belle Isle (Packard); Newfoundland (Jullien and Calvet); Gulf of St. Lawrence (Whiteaves). (*b*) *Coastal North America*: Point Barrow, Alaska to Puget Sound, Washington; Coburg Island, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Spitsbergen; Barents Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 0–1267 m.

Genus *Myriozoella* Levinsen, 1909

Myriozoella plana (Dawson, 1859) (Plate XIV, *a*)

Lepralia plana Dawson, 1859, p. 256.

Myriozoum planum Hincks, 1892, p. 157; Whiteaves, 1901, p. 99.

Schizoporella plana Nordgaard, 1906, p. 15; Osburn, 1912, p. 280.

Myriozoum crustaceum Osburn, 1923, p. 9D.

Myriozoella crustacea Osburn, 1932, p. 16.

Myriozoella plana Osburn, 1936, p. 542.

Material examined. — stations 11, 20, 21, 28, 33, 58, 126, 203, 208, 229, 231, 317, 406, 547, 553, 616, 722, 820, 828, 901, 58-33, 61-43.

Distribution. — (*a*) *Canadian*: northwest Baffin Bay (Nordgaard, Osburn); Fury and Hecla Strait, Frozen Strait, Hudson Bay, Hudson Strait, Labrador (Osburn); Gulf of St. Lawrence (Hincks, Dawson, Whiteaves). (*b*) *Coastal North America*: Point Barrow to Juneau, Alaska; Coburg Island, Baffin Bay to the Gulf of St. Lawrence. (*c*) *Elsewhere*: West and East Greenland; Iceland; Faeroes; Jan Mayen Island; North Norway; Spitsbergen; Barents Sea; White Sea; Kara Sea; Laptev Sea; East Siberian Sea; Chukchi Sea; Sea of Okhotsk; Sea of Japan.

Bathymetric range: 1–406 m.

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(PLATES I–XIV *follow*)

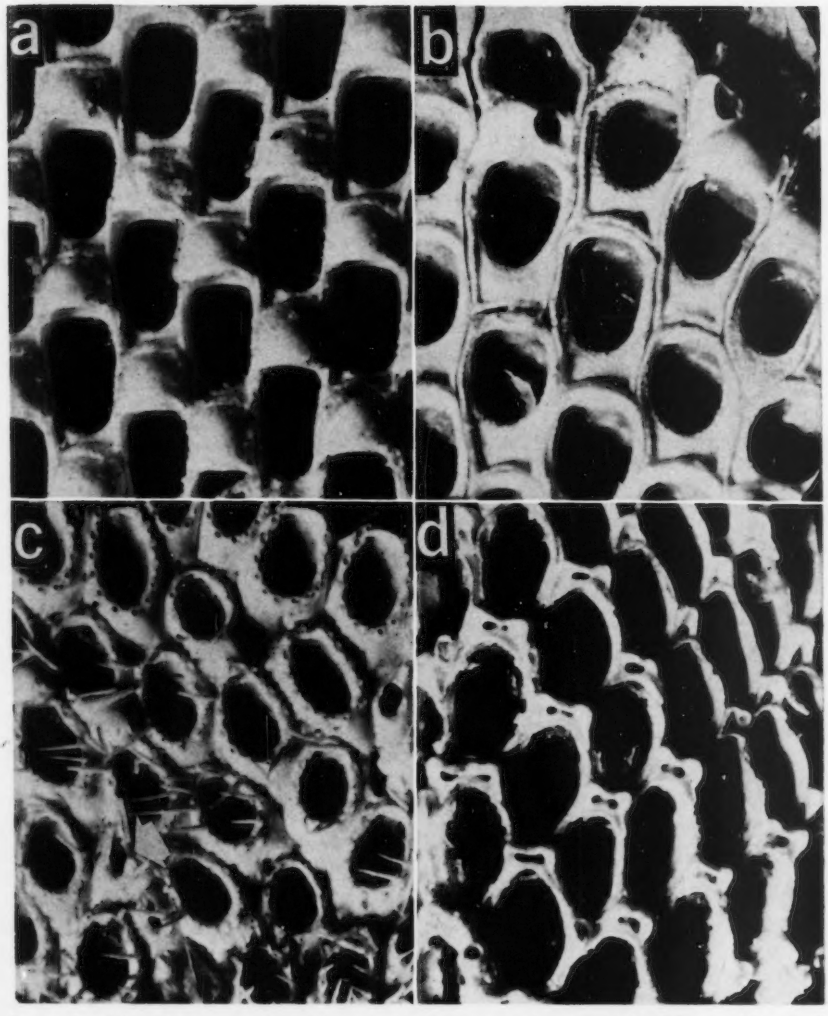

PLATE I. (*a*) *Bidenkapia spitzbergensis*. Hudson Strait (station 221). Colony with ovicells. (*b*) *Bidenkapia spitzbergensis*. Note the large avicularium transversely oriented along the proximal margin of the zooid; another avicularium is fused to an ovicell. Same colony as in (*a*). (*c*) *Copidozoum smitti*. Cumberland Sound (station 413). Colony with ovicells, an interzooecial avicularium is indicated. (*d*) *Hincksina nigrans*. Cape Parry Harbour (station 62-049). Colony with bilobate ovicells. Unless otherwise indicated all figures are magnified ×30.

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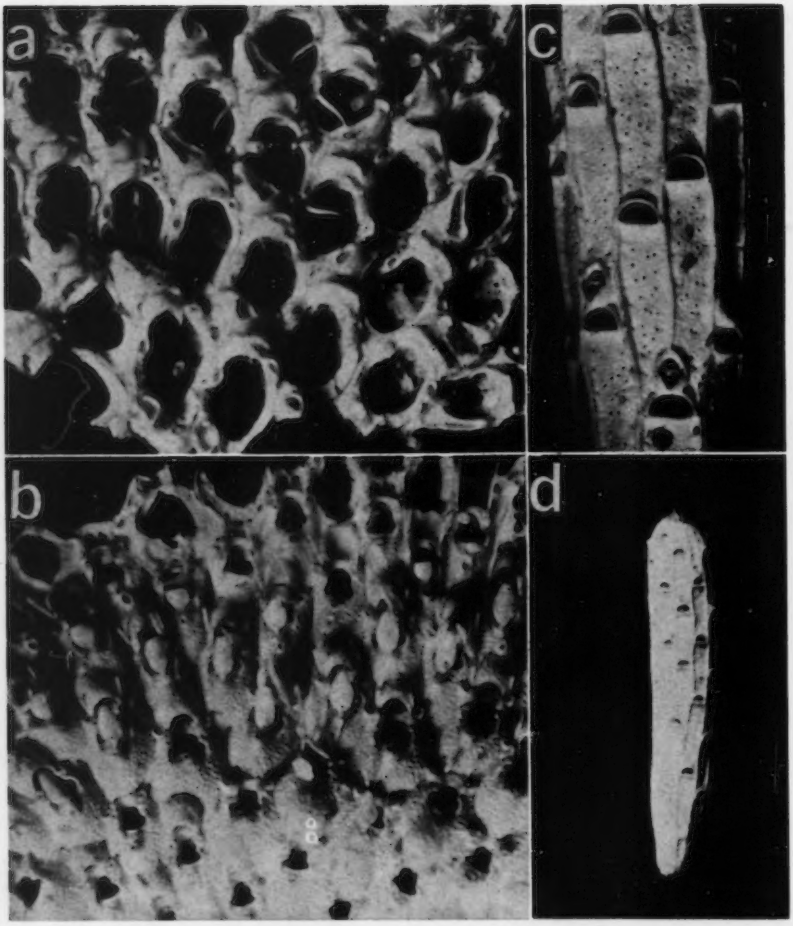

PLATE II. (*a*) *Tegella armifera*. West Hudson Bay (station 553). Colony with ovicells. (*b*) *Doryporella spathulifera*. Cumberland Sound (station 413). Colony with ovicells; note the jointed lanceolate frontal spines and the small adventitious avicularia. (*c*) *Microporina articulata*. Roes Welcome Sound (station 61-24). Portion of a node, comprising ordinary zooids. (*d*) *Microporina articulata*. Same colony as (*c*). ×9.

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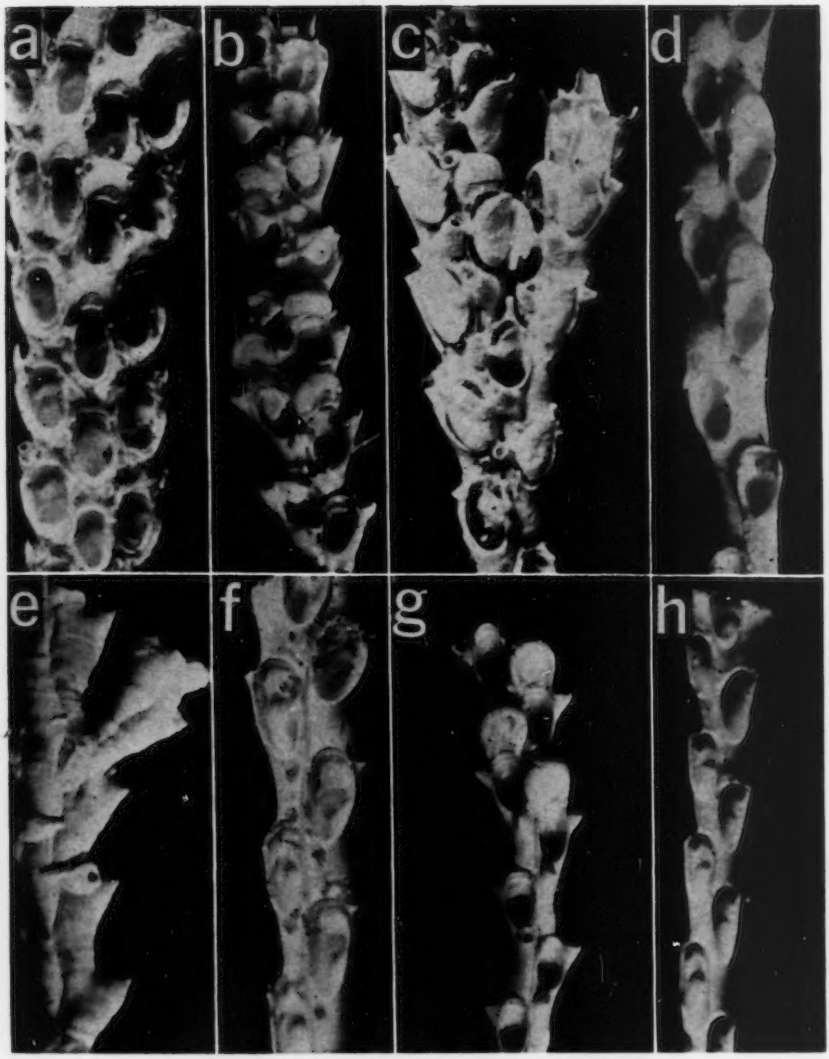

PLATE III. (*a*) *Caberea ellisii.* Northeast Hudson Bay (station 520). Portion of a branch; ovicells, with the inner wall of ectoecium exposed. (*b*) *Scrupocellaria scabra.* Belle Isle Strait (station 65–1502). Portion of a node with ovicells. (*c*) *Scrupocellaria scabra var. paenulata.* Frobisher Bay (station 331). Portion of two internodes, note the large frontal scutes. (*d*) *Tricellaria gracilis var. inermis.* Ellef Ringnes Island (N.M.C. No. 245). Portion of an internode with ovicells. (*e*) *Scrupocellaria scabra.* Basal view, showing two vibraculoid chambers, each with a rootlet pore. Same colony as in (*b*). (*f*) *Scrupocellaria arctica.* Northeast Ungava Bay (station 58). Portion of an internode taken from the proximal part of a colony. (*g*) *Notoplites smitti.* Melville Sound (station 65-1044). Portion of an internode with ovicells. (*h*) *Tricellaria peachii.* Frozen Strait (station 61-43). Portion of an internode.

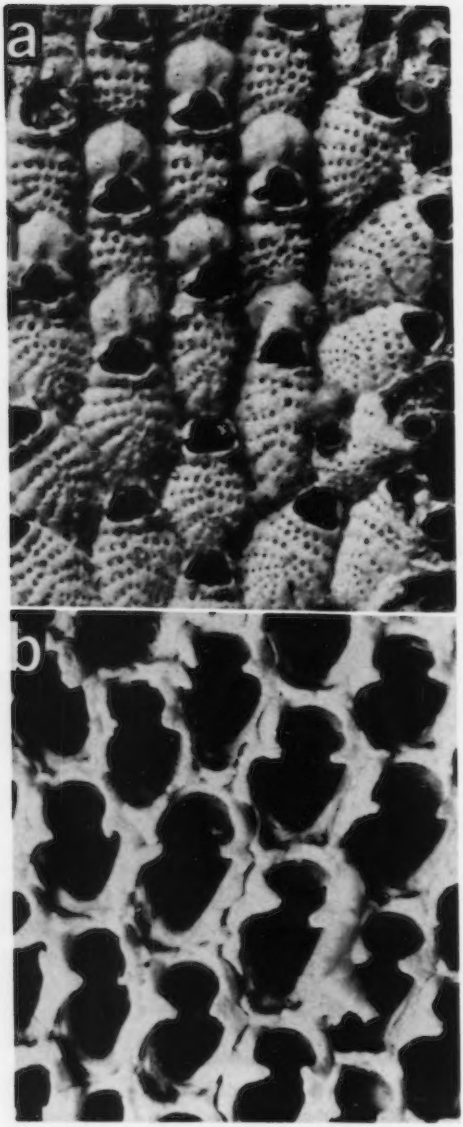

PLATE IV. (*a*) *Reginella spitzbergensis*. West Ungava Bay (station 126). Colony with ovicells. (*b*) *Membraniporella crassicosta*. Frobisher Bay (station 406).

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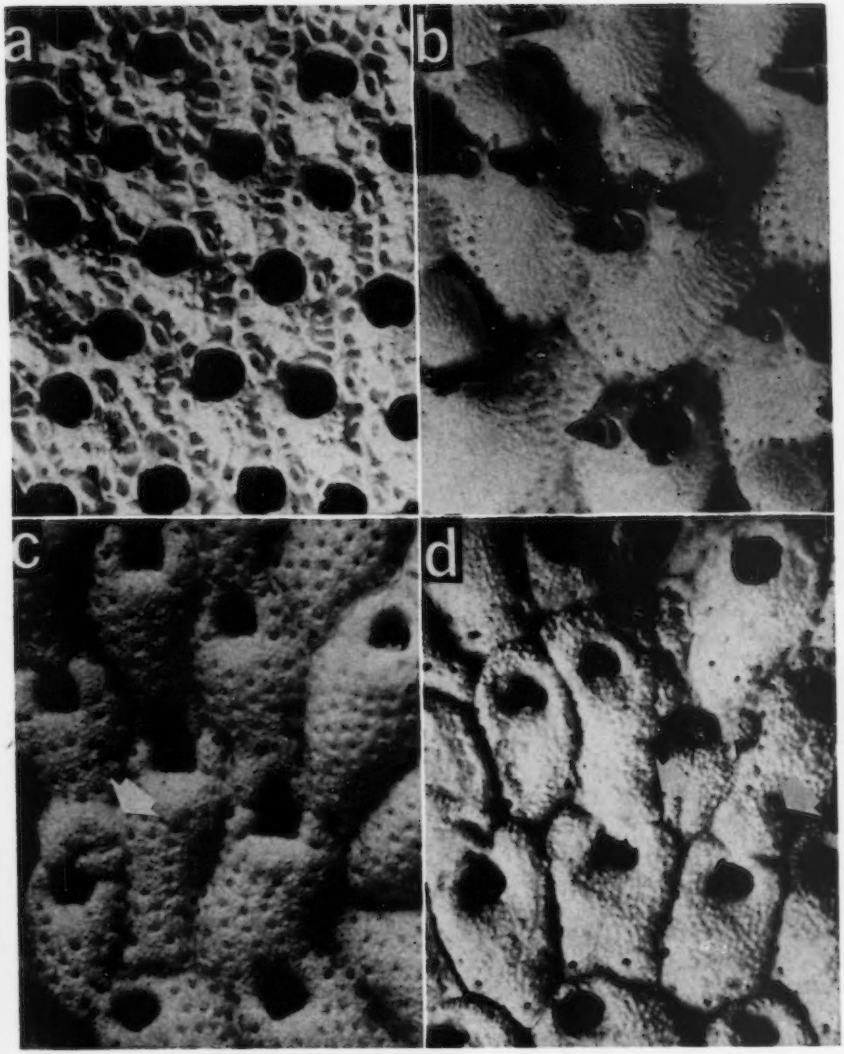

PLATE V. (*a*) *Umbonula arctica*. Roes Welcome Sound (station 61-26). (*b*) *Escharoide jacksoni*. East Somerset Island (station 62-2032). Colony with ovicells. (*c*) *Pachyegi sproducta* Caribou Island, Belle Isle Strait. Part of Packard's type material (M.C.Z.). Ovicell indicated. (*d*) *Hincksipora spinulifera*. Belle Isle Strait (station 65-1506). Ovicells indicated.

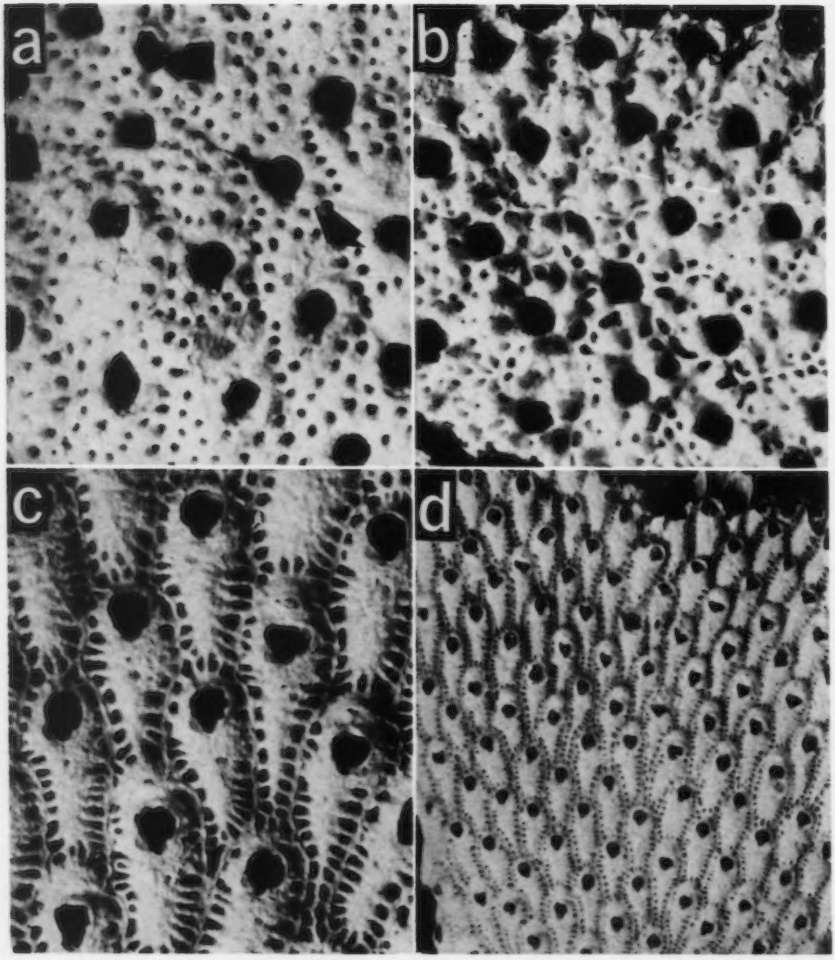

PLATE VI. (*a*) *Stomachetosella hincksi* n.sp. Belle Isle Strait (station 65-1505). Holotype. N.M.C. No. 756. Ovicell indicated. (*b*) *Stomachetosella cruenta*. Southwest Ungava Bay (station 203). Note the nodulate calcification of the frontal wall. (*c*) *Posterula sarsi*. Foxe Basin (station 811). Colony with ovicells. (*d*) *Posterula sarsii*. Same colony as in (*c*). ×10.

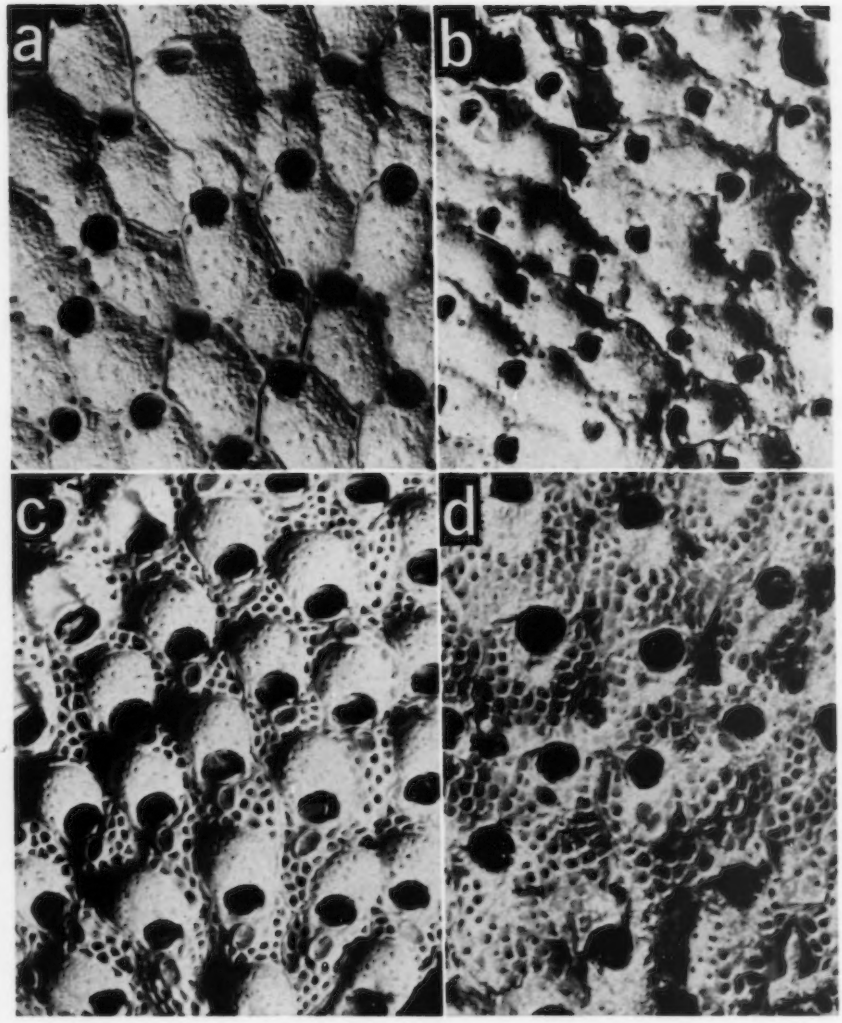

PLATE VII. (*a*) *Schizoporella stylifera*. Foxe Basin (station 61-32). Colony with ovicells. (*b*) *Schizoporella obesa*. North Hudson Bay (station 549). Ovicell indicated. (*c*) *Hippoporina reticulatopunctata*. Roes Welcome Sound (station 61-26). Colony with ovicells (*d*) *Hippoporina cancellata*. East Ungava Bay (station 33).

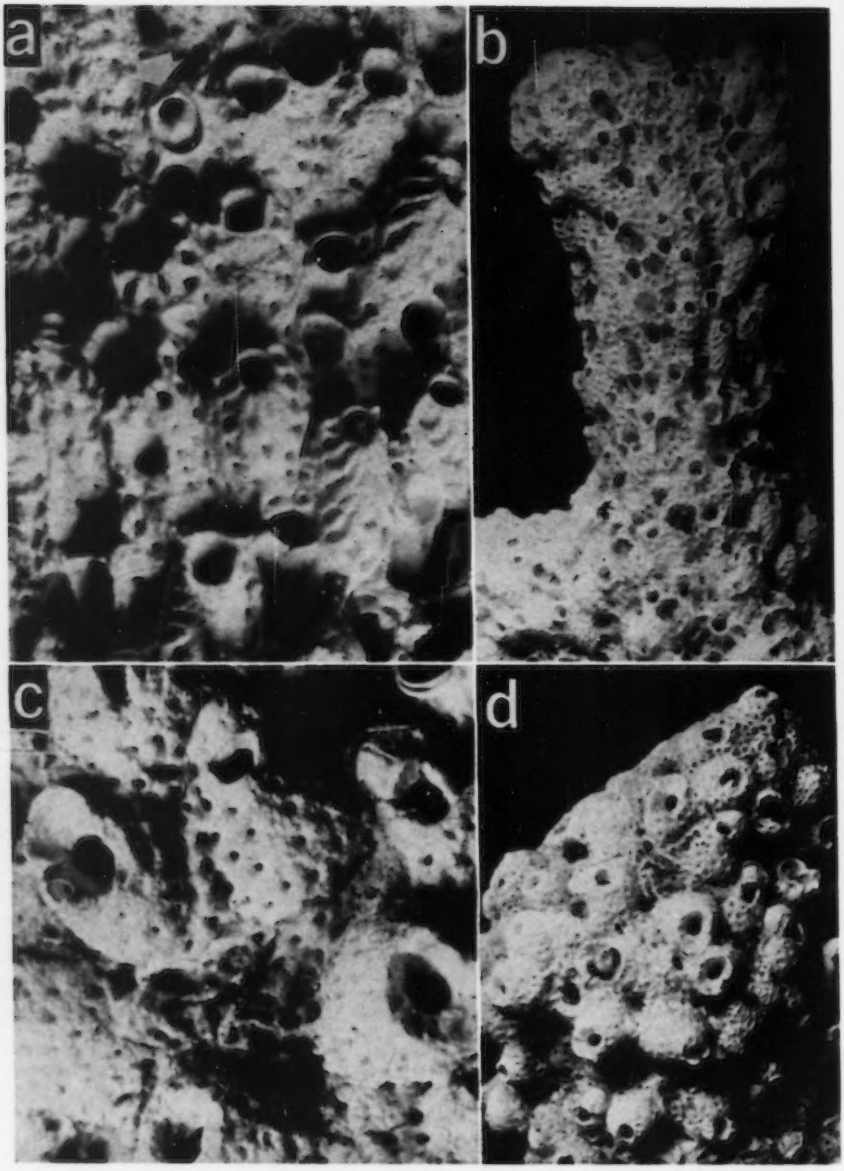

PLATE VIII. (*a*) *Celleporina surcularis*. North Hudson Bay (station 547). An interzooecial avicularium is indicated. (*b*) *Celleporina surcularis*. Same colony as in (*a*). ×10. (*c*) *Celleporina ventricosa*. Northwest Hudson Bay (station 61–8). Colony with ovicells. (*d*) *Celleporina ventricosa*. Same colony as in (*c*). ×10.

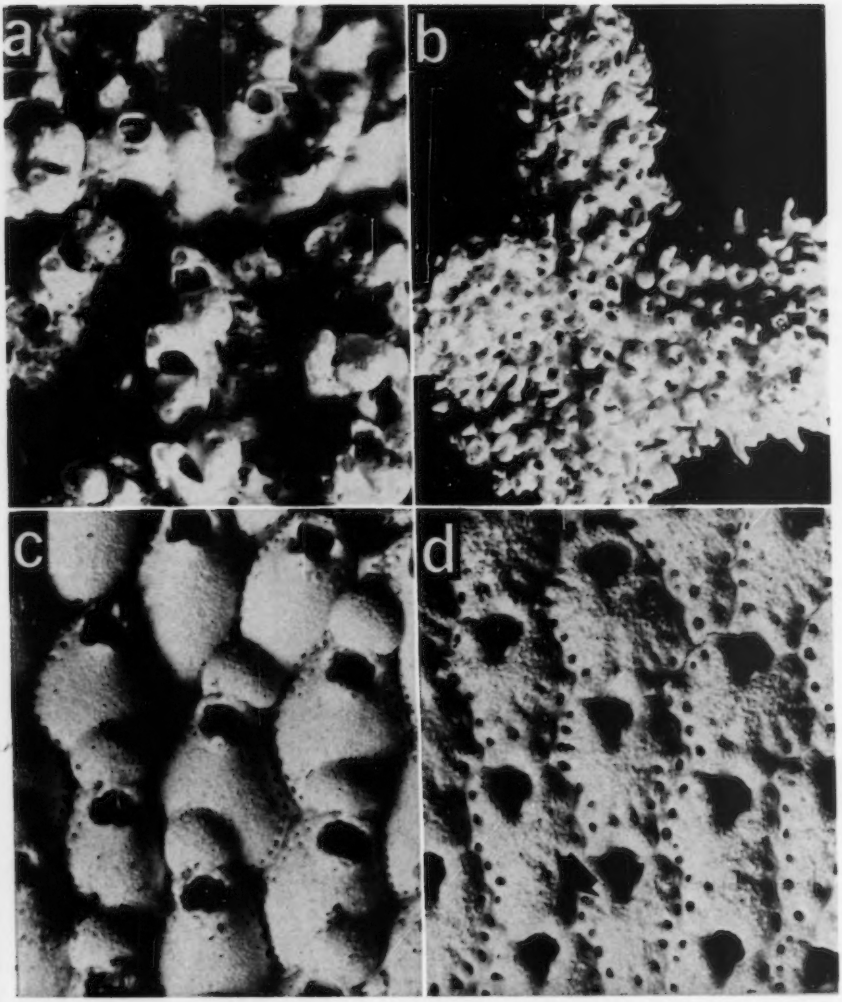

PLATE IX. *Schismopora nodulosa*. North Hudson Bay (station 547). Colony with ovicells. (*b*) *Schismopora nodulosa*. Same colony as in (*a*). ×10. (*c*) *Escharella ventricosa*. West Ungava Bay (station 126). Colony with ovicells. (*d*) *Escharella thompsoni*. Belle Isle Strait (station 65-1506). Colony with ovicells (one indicated).

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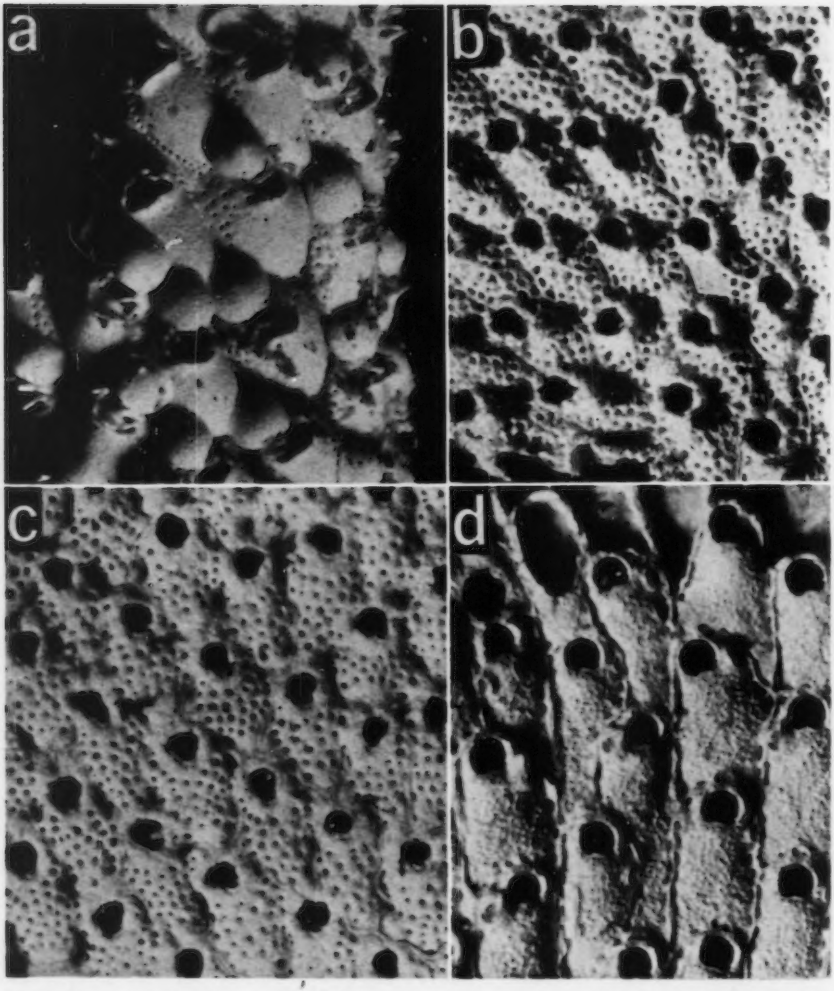

PLATE X. (*a*) *Escharella connectens*. East Ungava Bay (station 232). Colony with ovicells. (*b*) *Smittina mucronata*. East Ungava Bay (station 231). Ovicell indicated. (*c*) *Smittina rigida*. West Ungava Bay (station 126). Colony with ovicells. (*d*) *Parasmittina jeffreysi*. West Ungava Bay (stations 20, 21). Ordinary zooids at the growing margin of the colony.

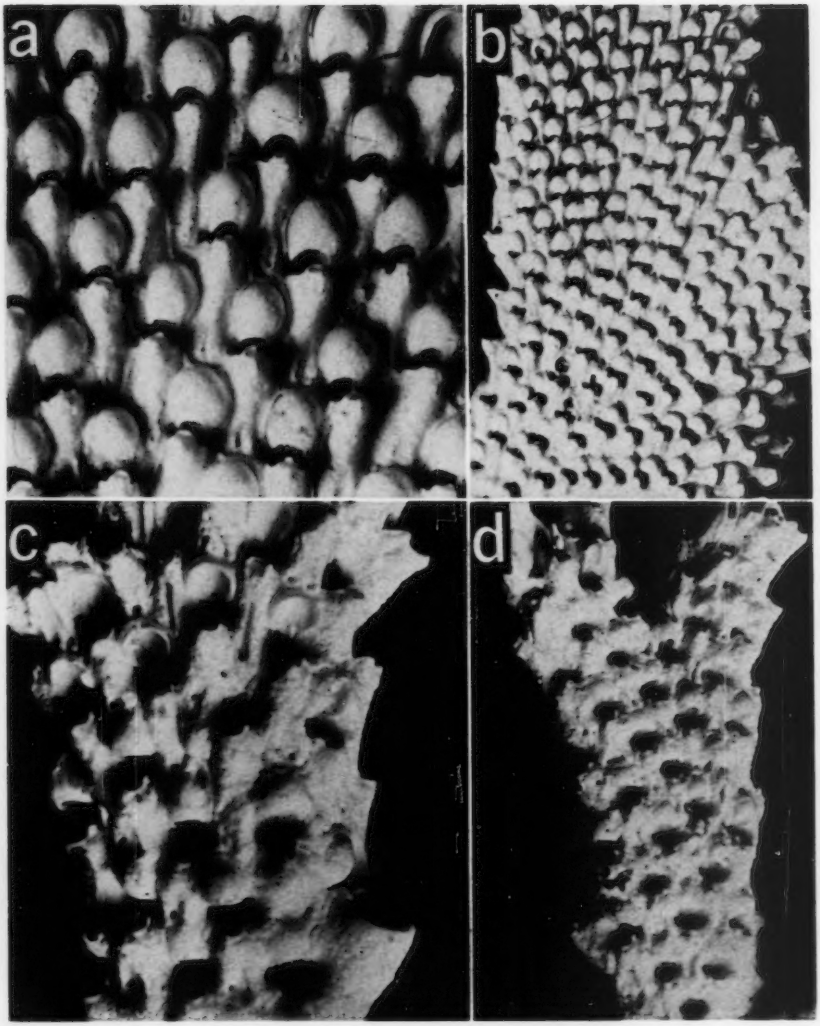

PLATE XI. (*a*) *Cystisella saccata*. Foxe Basin (station 818). Colony with ovicells. Note the prominent avicularian chambers. (*b*) *Cystisella saccata*. Same colony as in (*a*). ×10. (*c*) *Cystisella elegantula*. Northwest Hudson Bay (station 61–8). Colony with ovicells; note the gigantic lateral avicularia. (*d*) *Cystisella elegantula*. Same colony as in (*c*). ×14.

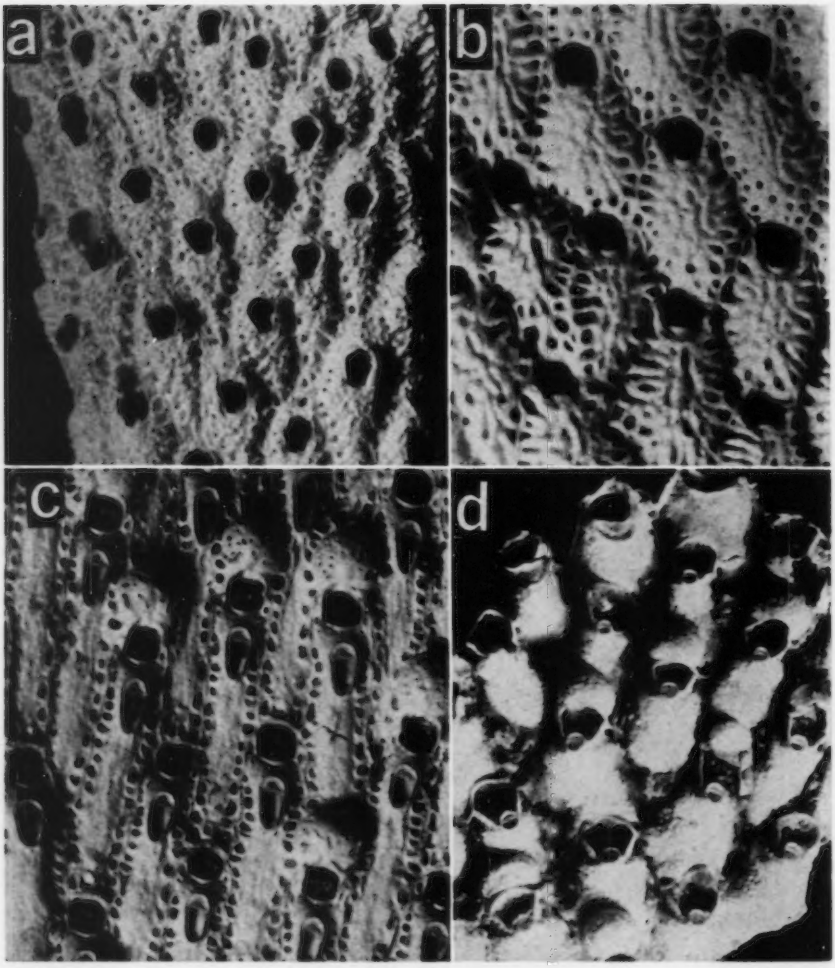

PLATE XII. (*a*) *Porella compressa*. Frobisher Bay (station 334). Colony with ovicells. (*b*) *Porella struma*. Belle Isle Strait (station 65-1510). (*c*) *Pseudoflustra solida*. Southeast Hudson Bay (station 54-49). Colony with ovicells. (*d*) *Porella aperta*. East Somerset Island (station 62-2031). Colony with ovicells.

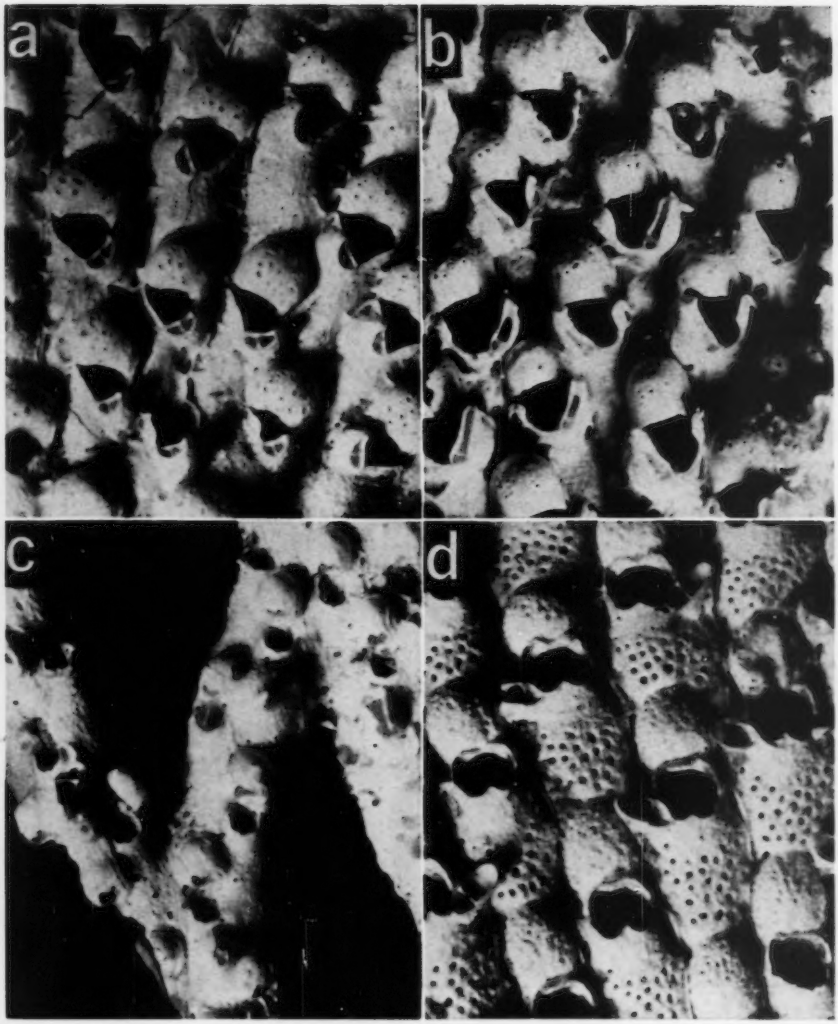

PLATE XIII. (*a*) *Rhamphostomella hincksi*. Foxe Basin (station 723). Colony with ovicells. (*b*) *Rhamphostomella plicata*. Frobisher Bay (station 319). Colony with ovicells. (*c*) *Phidolopora elongata*. Mouth of Lake Harbour Fiord, Baffin Island. N.M.C. No. 251. Colony with ovicells. (*d*) *Cheilopora sincera*. East Somerset Island (station 62-2032). Colony with ovicells.

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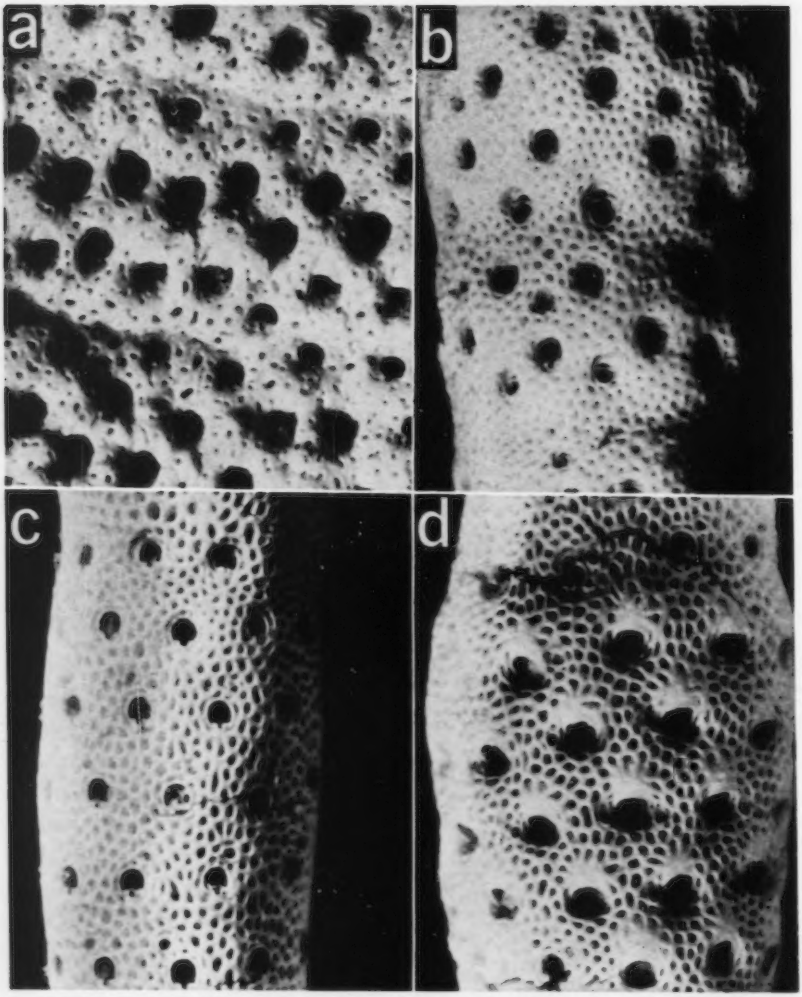

PLATE XIV. (*a*) *Myriozoella plana*. North Hudson Bay (station 616). Colony with ovicells. Narrow furrows comprising ordinary zooids separate broader areas of ovicelled zooids. (*b*) *Myriapora coarctica*. Northeast Ungava Bay (station 106). Portion of a nonovicelled node; note the large interzooecial avicularia which distinguish this species from *M. subgracila*. (*c*) *Myriapora subgracila*. Foxe Basin (station 61-32). Portion of a nonovicelled node. (*d*) *Myriapora subgracila*. Node with ovicells. Same colony as in (*c*).

Degradation of DDT in Atlantic Salmon (*Salmo salar*)[1]

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ABSTRACT

As indicated by thin-layer chromatography, hatchery-reared Atlantic salmon parr degraded DDT, absorbed from aqueous suspensions, to DDE and TDE within 9 hr. DDT adsorbed on external surfaces of the salmon was not degraded.

INTRODUCTION

Analyses of the tissues of numerous species of fish have shown that fish often contain not only the insecticide DDT but also two of its metabolites, namely DDE and TDE (Dustman and Stickel, 1966), that are less toxic than DDT (Rudd and Genelly, 1956). Atlantic salmon (*Salmo salar* L.), one of the species occurring in DDT-contaminated watersheds (J. R. Macdonald, 1965; MacDonald and Penney, 1967), has been shown repeatedly to contain metabolites of DDT. Anadromous salmon parr taken from the Taxis and Southwest Miramichi rivers of New Brunswick contained DDT, DDE, and TDE (D. R. MacDonald, 1965), and landlocked Atlantic salmon from Sebago Lake in Maine contained DDT and DDE (Anderson and Everhart, 1966). The metabolite DDE alone was found in Atlantic salmon parr from the Highlands of Scotland where DDT is known to have been applied to sheep (Holden, 1966) whereas, curiously, unmetabolized DDT was found in Irish Atlantic salmon, notwithstanding that the DDT was unlikely to have been acquired locally, from sources in Ireland (Eades, 1966).

Despite the presence of DDE and TDE in fish, little is known conclusively about the ability of fish to degrade DDT. According to Holden (1966), it is more probable that fish acquire the metabolites together with their foods, after the degradation of DDT in some of the early stages of the food chains. On the other hand, experimental evidence exists for the metabolism of DDT by three species of salmonid fish: Atlantic salmon, cutthroat trout, and rainbow trout. Premdas and Anderson (1963) suggested that DDT was detoxicated by degradation within the bodies as well as on the external surfaces of young Atlantic salmon. The toxicity of C^{14}-labeled residues of DDT, extracted from the tissues of salmon that had absorbed labeled DDT from water, had decreased to 36% of that of DDT; the toxicity of externally adsorbed residues, obtained by rinsing the salmon with acetone, had decreased to 92% of that

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of DDT. However, as the existence of the suspected metabolites of DDT in the extracts was not confirmed through chemical analysis, Premdas and Anderson (1963) stressed that the detoxication might not have resulted from the degradation of DDT, but that some of the extracted DDT could have been rendered nontoxic through binding to other molecules.

Cutthroat trout, exposed intermittently to DDT for 20 months, accumulated DDE in amounts sufficient to indicate that the metabolite originated from the degradation of DDT in the fish (Allison et al., 1963, 1964). However, since the concentrations of TDE in the trout remained low enough to have been taken up from a TDE-contaminated diet, Allison et al. expressed doubt that cutthroat trout metabolized DDT to TDE.

Wedemeyer (1968) found both DDE and TDE in the blood and livers of rainbow trout that had been administered DDT. As the DDT was converted to DDE at a higher rate in trout that had been given DDT by gavage than in those that had received DDT by injection, some degradation of the DDT likely occurred in the digestive tracts of the trout. Rainbow trout liver was suggested by Wedemeyer as another organ of DDT metabolism, because DDT became degraded to DDE in trout liver homogenates.

Although the toxicity of DDT residues in Atlantic salmon has been shown to decrease, the question of DDT metabolism in the salmon remains incompletely resolved. The study reported here was undertaken to identify chemically the DDT residues in Atlantic salmon parr that were killed in aqueous suspensions of DDT.

GENERAL MATERIALS AND METHODS

All salmon used in this study were yearling parr, reared at the Florenceville Fish Culture Station, N.B., that were conditioned for at least 60 days at 12–16 C in flowing water in the laboratory. The parr were given daily about 0.2 g of raw, finely ground beef liver per gram of fish.

To expose the parr to DDT, groups of unfed fish were kept in 7-liter glass jars containing 6 liters of aerated aqueous suspensions of *p,p'*-DDT (1,1,1-trichloro-2,2-bis(*p*-chlorophenyl)ethane) (Fisher Scientific Co.) at 12–16 C. Every dying fish was removed from the jars as soon as movements of its body, fins, and gills ceased. After draining, the fish were cut into pieces and, to prevent post-mortem decomposition of absorbed DDT (Barker and Morrison, 1964), these were digested without delay in the glacial acetic–perchloric acid digestion mixture of Stanley and LeFavoure (1965). However, to permit complete digestion of the tissues at 60 C rather than at the usual 100 C, the concentration of the perchloric acid was increased from 60 to 70%, and 2.5 ml instead of 2.0 ml of the digestion mixture were used per gram of tissue. Thus, each digestion was completed in 3 hr. The acid digests of all parr from each test group were pooled.

Fats in the acid digests were extracted with petroleum ether. DDT residues were freed from the fats in a sulfuric acid-Celite 545 cleanup column (Association of Official Agricultural Chemists, 1960, sec. 24, p. 111; Stanley

and LeFavoure, 1965); collected in a centrifuge tube; and dried by evaporation at 60 C. Prior to their analysis, the residues were dissolved again in 200 μliters of petroleum ether.

In preparation for thin-layer chromatography, glass plates (20 × 20 cm) were coated with a 250-μ layer of aluminium oxide G (E. Merck AG.) from which possible residual chlorides were removed by washing with a mixture of acetone and distilled water (Kovacs, 1963). The chromatography plates were activated for 1 hr at 105 C. DDT and its degradation products were separated by spotting 100-μliter samples of the dissolved residues at the lines of origin on the chromatography plates and by developing the plates in a solvent, consisting of a 4% (v/v) solution of heavy mineral oil in petroleum ether. To make the separated metabolites of DDT visible, the chromatographic plates were sprayed with Mitchell's chromogenic agent (Mitchell, 1958) and exposed to shortwave ultraviolet radiation until the appearance of colored spots.

Characteristic R_f values for *p,p'*-DDT, *p,p'*-DDE (1,1-dichloro-2, 2-bis(*p*-chlorophenyl)ethylene), and *p,p'*-TDE, (DDD; 1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethane), about 0.69, 0.79, and 0.40 respectively, were established by repeating the chromatographic procedure with 0.15% standard solutions of each of the three metabolites in petroleum ether. The standards, 30 μliters of each, were spotted in combinations (Fig. 1, A) as well as singly. As an added precaution, the standards were developed on every chromatogram of the extracted DDT residues.

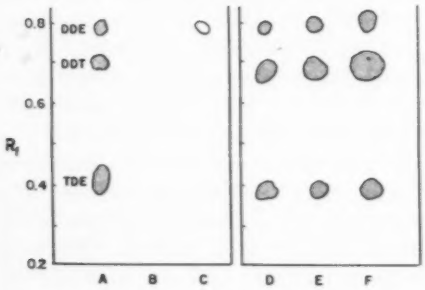

FIG. 1. Tracings of parts of two chromatograms of tissue extracts. *Left*: A, standards; B, beef liver; C, salmon before exposure to DDT. *Right*: salmon after death in aqueous suspensions of *p,p'*-DDT: D, 0.01 ppm, 23 hr; E, 0.1 ppm, 75 hr; F, 2.0 ppm, 9 hr.

Since the parr used had been reared in a hatchery where they might have received some DDT from hatchery water or from food, and since they had been fed on a diet of liver while in the laboratory, it was necessary to determine whether the parr or the liver contained any DDT or its metabolites before the parr were exposed to DDT intentionally. For this purpose, a group of 10 parr and an approximately 31-g piece of beef liver from the local abattoir were digested and analyzed.

After an hour of exposure to ultraviolet, a very faint spot of what appeared to be *p,p'*-DDE (Fig. 1, C) became visible on the chromatogram of the parr extract. Clearly, the parr had had some previous exposure either to DDT

or directly to DDE. As no perceptible spots developed on the chromatogram corresponding to the liver extract (Fig. 1, B), the liver given to the fish appeared to be free from DDT and its metabolites, at least as far as could be detected by the method of analysis used.

EXPERIMENTS

To determine whether the parr could degrade DDT taken up from water, three groups of fish were exposed to different concentrations of *p,p'*-DDT. The largest group, consisting of 20 parr with an average weight of 2.5 g, was killed in about 9 hr by an aqueous suspension of 2.0 ppm *p,p'*-DDT, the highest concentration used. Nine parr of the same size-group died in about 75 hr while in a 0.1-ppm suspension. Seven smaller parr (average about 1.4 g), kept in a 0.01-ppm suspension, died in about 23 hr.

Three spots of DDT residues, corresponding to the R_f levels of *p,p'*-DDT, *p,p'*-DDE, and *p,p'*-TDE, were separated (Fig. 1, D–F) from the extracts of each of the three groups of parr, analyzed simultaneously on one chromatography plate. Despite the differences in the concentrations of DDT to which the different groups had been exposed and in the durations of exposure, all developed spots on the chromatogram were not only clearly visible but dense. The large areas of the spots from the fish extracts, compared with the areas of the spots from the strandard solutions and with the faint spot of DDE from the fish before exposure to DDT, indicated that the parr had taken up considerable quantities of DDT from the suspensions and had degraded a substantial proportion of the DDT to DDE and TDE.

The next experiment was designed to test the possibility that some DDT, adsorbed on the external surfaces of the parr, might have been degraded before its absorption by the parr. Therefore, a group of 20 2.5-g parr was exposed to a suspension of 2.0 ppm *p,p'*-DDT in water. After their death in about 9 hr, 10 parr were digested whole, exactly as in the previous experiment. However, before the acid digestion of the remaining 10 parr, the body and gill surfaces of each fish were rinsed with 10 ml of acetone that was pooled in a beaker and evaporated. The dry residue was redissolved in 10 ml of petroleum ether and purified in an acid-Celite column. The extracts from the surface washes, from the bodies of the washed whole parr, and from the unwashed parr were separated chromatographically. The entire procedure was repeated with a second group of 20 parr.

The extracts from each group of whole fish, washed as well as unwashed, separated on the chromatograms as *p,p'*-DDT, *p,p'*-DDE, and *p,p'*-TDE, as in the earlier experiment. The material obtained from the surfaces of the parr appeared to contain DDT only, because the only spot that became visible on each chromatogram of the surface washes had migrated the distance that was characteristic of *p,p'*-DDT. Thus, as far as could be demonstrated by the method employed, the degradation of DDT to DDE and TDE was confined to sites within the fish.

DISCUSSION

The marked increase in the density and size of the chromatographic spots of DDE that developed after only 9 hr of absorption of DDT by the salmon, compared with the trace of DDE that the fish had accumulated from undetermined sources before the experiment, is indicative of rapid dehydrochlorination of DDT. The equally abrupt appearance of TDE in the salmon probably indicates the existence of another, rapidly operating mechanism of dechlorination of DDT in the fish. That DDT may be degraded in Atlantic salmon even more rapidly than was suggested in this study can be deduced from the measurements of Premdas and Anderson (1963) who found that considerable quantities of water-borne DDT not only entered Atlantic salmon in about 5 min but became partly nontoxic in the same period.

With regard to the fact that some analyses of wild Atlantic salmon have shown the presence of DDE, even if TDE was not detectable in the same fish (Anderson and Everhart, 1966; Holden, 1966), it should be noted that DDE is the particular metabolite of DDT that tends to accumulate in other vertebrates, apparently because it is excreted more slowly than TDE (Hayes, 1965; Stickel et al., 1966). Therefore, salmon and other species of fish, if they absorb DDT in small doses, may store some DDE while eliminating TDE almost as rapidly as it is produced. This appears to have happened during the prolonged experiments by Allison et al. (1963; 1964), in which cutthroat trout accumulated little TDE.

Whether DDT can be metabolized in fish to more compounds than DDE and TDE remains unknown because no one appears to have isolated further metabolites from fish. This possibility should be considered, nonetheless, since other metabolites of DDT have been identified from homeothermic vertebrates, e.g., seven compounds were extracted from rats (Peterson and Robinson, 1964).

Although Premdas and Anderson (1963) envisaged possible degradation of DDT on the external surfaces of Atlantic salmon, we could not corroborate this. On the basis of their suggestion that acetone, used to rinse the surfaces of the salmon, may have extracted some DDT metabolites from the tissues of the fish, at least some traces of DDE and TDE should have become visible on the chromatograms of the rinses during our experiment. As only DDT was isolated by us from the rinses, it seems more likely that not all adsorbed DDT can be washed from the mucus on fish surfaces in a form completely free to exhibit its toxicity. Instead, since DDT is hydrophobic and tends to adhere to nonaqueous surfaces (Bowman et al., 1959), some of it may be held captive, and apparently nontoxic, among loosened mucus particles.

ACKNOWLEDGMENTS

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Occurrence and Significance of Iron, Manganese, and Titanium in Glacial Marine Sediments from the Estuary of the St. Lawrence River[1]

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ABSTRACT

In glacial marine sediments from the St. Lawrence estuary, iron varies between 1.32 and 5.42%, manganese between 0.043 and 0.28%, and titanium between 0.31 and 0.64%. The regional distributions of these elements are related to sediment texture. Analyses of individual sediment size-fractions show that Fe, Mn, and Ti concentrations generally increase with decreasing grain size. Variations in elemental ratios between the different grades suggests that not all of the Fe and Mn is located in detrital silicate minerals. Dithionite extraction of selected sediments resulted in preferential dissolution of 3–16% of the total iron, presumably that derived from amorphous and crystalline iron oxides and from sorbed material.

Hydroxylamine–hydrochloride removed 5–60% of the total manganese, presumably that derived from exchangeable Mn, easily reducible Mn oxides, and sorbed Mn material. The soluble fraction is highest in freshly deposited pelites from the center of the estuary. Soluble Fe and Mn occur as oxide films on the particles deposited from suspension, and the amount held depends on rate of deposition and on the physicochemical conditions in the waters and in the sediments. In contrast, Ti occurs in detrital minerals and accumulates at the same rate as detrital sedimentary material. It is unaffected by environmental changes. This investigation shows that, despite the derivation of the sedimentary material from the Canadian Shield predominantly by nonchemical erosional processes, small but significant chemical modification of iron- and manganese-bearing material is taking place in response to present physicochemical conditions.

INTRODUCTION

Very little is known of the chemistry of glacial marine sediments, but they can sometimes provide an excellent opportunity for studying the response of relatively unaltered crystalline detrital material to marine physicochemical conditions.

A geochemical study by Nota and Loring (1964) showed that many of the elements such as Si, Al, Na, and K and their host minerals in glacial marine sediments from the St. Lawrence estuary are not affected by the marine environment, but iron and manganese appeared to be more sensitive to it. Studies were, therefore, made on the abundance and distribution of iron, manganese, and titanium in the St. Lawrence estuary. The purpose of this study was to determine the processes by which iron and manganese are incorporated into

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marine sediments and to compare their responses to physicochemical conditions with that of titanium, another element usually unaffected by environmental changes.

This study forms part of a series of geochemical investigations which are being carried out by the Marine Ecology Laboratory of the Fisheries Research Board of Canada.

GEOLOGIC AND GEOCHEMICAL FRAMEWORK

The St. Lawrence estuary (Fig. 1) is bounded to the north by Pre-Palaeozoic granites, syenites, granodiorites, anorthosites, gneisses, and schists of the Canadian Shield, and to the south by the folded Palaeozoic limestones, calcareous sandstones, shales, and slates of Gaspé Peninsula (Harrison, 1963).

Anticosti Island (a limestone cuesta) is separated from the north shore by the shallow Jacques Cartier Passage, and from the Gaspé Peninsula by the deep Gaspé Passage. The central part of the estuary is occupied by a deep, glacially modified submarine trough known as the Laurentian trough. Narrow shelves border the trough except where the northern shelf widens into a broad bank-and-basin type of topography southeast of Sept Iles.

The marine sediments are made up of varying admixtures of gravel, sand, silt, and clay (for sedimentary nomenclature see Nota, 1958). Deepwater pelites occur at depths greater than 150 fath. They are dark greenish-grey below the sediment–water interface, and dark yellowish-brown at the interface (Munsell rock colour chart, 1951; 5GY 5/1, 10 YR 4/2). The average clay content is about 60% by weight and the silt content about 35%. Most samples contain a small quantity of sand and gravel. The pelite is supplied in suspension after thorough mixing in the saline waters of the Gulf, and is derived from the drainage area of the St. Lawrence River and also from the surrounding land area. Sandy pelites occur on the upper slopes of the trough and on the offshore parts of the shelves whereas nearshore sediments are mainly sands and pelitic sands. In areas where the bottom topography is rugged (e.g. southeast of Sept Iles), gravels, sands, pelitic sands, and sandy pelites occur on the banks whereas, in the intervening basins, deposits referred to as the protected basin type of pelite occur. These sediments are mainly derived from the reworking of older glacial deposits and by ice-rafting from the shorelines.

Heavy and light minerals in the sediments reflect their original provenance among the igneous rocks of the adjacent Shield area. Appreciable quantities (5–13% by weight) of heavy minerals occur in the sand size-fraction irrespective of geographical location. Although heavy minerals are present in the whole sand-fraction studied (500–50 μ), they predominate in the 200–80 μ size-fraction. This heavy mineral suite is characterized by the abundance of relatively unstable minerals such as hornblende and pyroxene. Hornblende and pyroxene rich in Fe and Mn with some Ti may make up 60% of the transparent heavy minerals, whereas epidote, titanite, rutile, apatite, biotite, and olivine are present in minor quantities. Stable minerals such as tourmaline and zircon are either present in very low concentrations

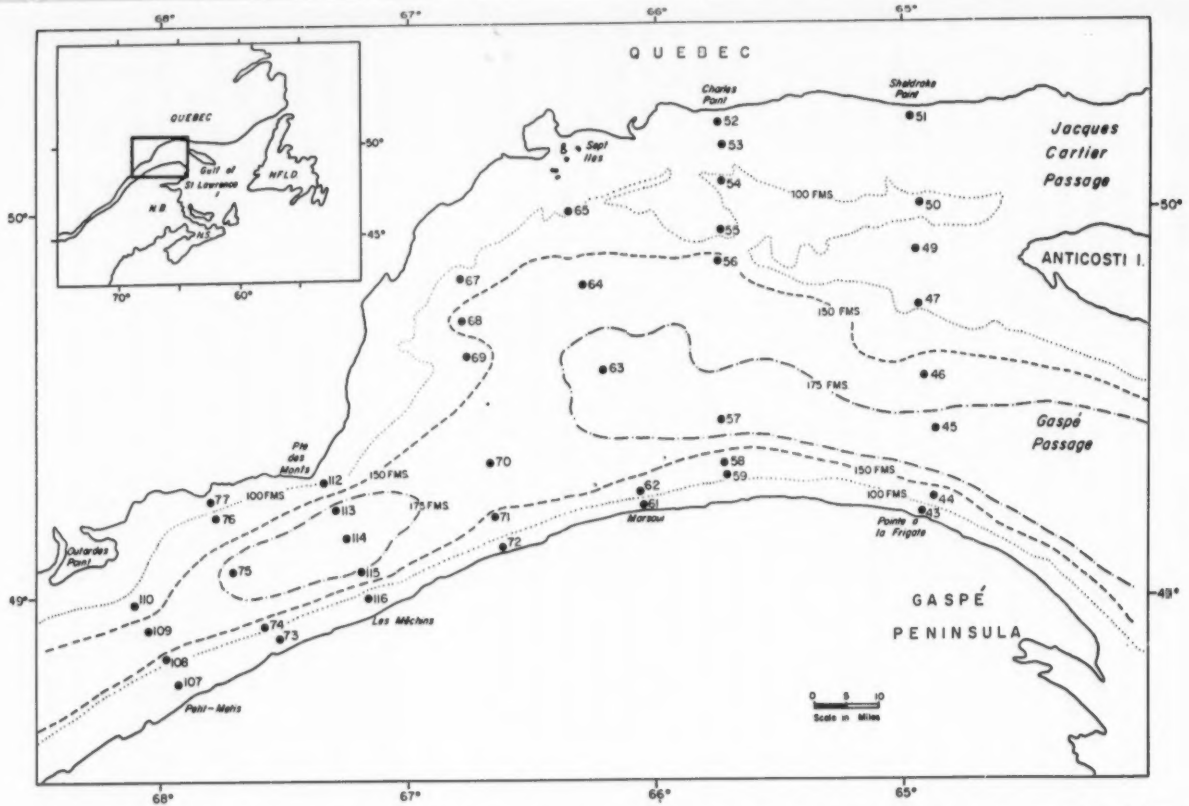

FIG. 1. Locations of sampling stations (●) in the St. Lawrence estuary. Generalized bathymetry of the Laurentian trough in fathoms is based on data from Canadian Hydrographic Service Chart 4002. Insert map shows the location of the study area. Place names referred to in text are also shown.

or are absent. The light mineral suite is predominantly plagioclase feldspar (41%) with lesser amounts of quartz (34%) and potash feldspar (16%). These primary silicate minerals have escaped chemical decomposition and have been deposited in even the finest size-fraction. The clay size-fraction contains plagioclase feldspar (mainly oligoclase), amphibole, pyroxene, and chlorite in addition to the major constituents: quartz, illite, and kaolinite.

The waters of the estuary are completely marine (salinity ranges from 27 to 34‰). Oceanographic conditions, however, are complex as a result of the mixing of water masses of acutely contrasting temperature and salinity (Hachey et al., 1956). Seasonal and unseasonal variations in temperature and salinity occur throughout the water column (Lauzier and Bailey, 1957; Hachey, 1961). Generally, the waters of the estuary are well oxygenated. The concentration of dissolved oxygen decreases with depth. At the surface the dissolved oxygen content is about 8 ml/liter, whereas near the bottom it varies from 7.5 ml/liter in shallow parts to 1.8 ml/liter in deeper parts. Nowhere is bottom water stagnant. The acidity of the water ranges from *p*H 7.6 to *p*H 8.0. The *p*H is highest in the surface waters and lowest near the sediment–water interface.

Oxidizing conditions prevail at the sediment–water interface of the deep-water pelites. This was inferred from the presence of a thin (1–2 cm) brown layer at the interface, by qualitative chemical tests which showed that ferric iron was the predominant iron species in the surface layer, and by positive Eh values ($\geq$400 mv). Below the interface, reducing conditions prevail. This was inferred from the dark greenish-grey colour of the sediments, by chemical tests which showed that ferrous iron predominated, and by negative Eh values. The *p*H of the sediments varied from 6.89 to 8.12 with an average value of 7.30. There was no regional pattern of *p*H values.

FIELD AND LABORATORY METHODS

Sediment samples (Fig. 1) were obtained with a modified Van Veen grab (0.1 m^2) and short gravity corer. Field observations of fresh samples included the measurement of *p*H and Eh (Beckman Model G *p*H-Eh meter), oxygen activity ($KCNS/K_3Fe(CN)_6$ method of Jackson (1958, p. 354–357)) together with estimates of sediment colour (Munsell rock colour chart, 1951), and gross lithology. Water samples for determination of temperature, salinity, *p*H, and dissolved oxygen were collected at selected stations and at various depths.

Sedimentological analyses were carried out using standard techniques (see Nota and Loring, 1964, for details). Separation of the individual size-fractions was carried out after dispersion in 0.16 N, $NH_4(OH)$, and X-ray diffraction measurements of the clay size-fraction (<0.002 mm) of selected samples were made with a Noralco high angle X-ray diffractometer and a Phillips Powder Camera (Cu, K radiation).

Chemical analyses of the total sediment sample and individual size-fractions of selected samples for the oxides of Ti, Al, total Fe, and Mn were

made after removal of soluble sea salts by methods essentially similar to those of Riley (1958). Ferrous iron was determined by the method of Groves (1937) but ceric sulphate was used instead of $KMnO_4$. Additional determinations on selected samples were made to investigate the partition of iron and manganese among the soluble phases. Dithionite ($Na_2S_2O_4$) was used to remove amorphous and crystalline iron oxides and iron sorbed by sediment particles following the method described by Mehra and Jackson (1958). Hydroxylamine-hydrochloride (1% solution) was used to remove exchangeable Mn^{+2}, easily reducible manganese oxides, and iron sorbed by the sediments. Both treatments leave the lattice structure of the silicate minerals intact and do not attack the resistant oxides such as ilmenite and hasumannite (McKeaque and Day, 1966; Heintze and Mann, 1951). Iron and manganese in the dithionite and hydroxylamine-hydrochloride filtrates were determined by atomic absorption using a Perkin-Elmer Model 303 Atomic Spectrophotometer.

IRON

Total Iron

The iron (Fe) content (Fig. 2) varies between 1.32 and 5.42% (average 4.24%) and is regionally related to sediment texture. Low concentrations occur in sands and sandy pelites from nearshore areas and on topographic highs, whereas higher concentrations are found in deepwater pelites from the central part of the Laurentian trough. Chemical analyses of individual size-fractions (Tables I and II) indicate that the lower Fe contents of the coarser grained sediments are simply a reflection of their high sand component, whereas the higher Fe contents of the deepwater pelites are a reflection of their high fine silt and clay content.

Ferrous and Ferric Iron

Regionally, the Fe^{+3}/Fe^{+2} ratios decrease with decreasing grain size. Ferrous iron is the predominant component in the St. Lawrence estuary with concentrations varying from 1.45 to 2.38% (average 2.16%), whereas the ferric iron content varies between 0.88 and 3.18% (average 1.59%). Ferrous iron contents remain relatively constant and show no consistent relation to sediment texture or to location in the estuary. Ferric iron content, however, is related to changes in texture. Low Fe^{+3} values usually occur in the sands and sandy pelites of the nearshore areas whereas higher values are usually associated with the deepwater pelites from the central part of the trough, presumably because of some oxidation of this fine grained material.

Chemical Partition of Iron in the Sediment

Preferential dithionite extraction of sediments representative of the Laurentian trough (stations 55–59, Fig. 1) resulted in the dissolution of varying amounts of iron. This iron was probably derived from amorphous iron compounds, from crystalline oxides, and from sorbed material. Dithionite soluble

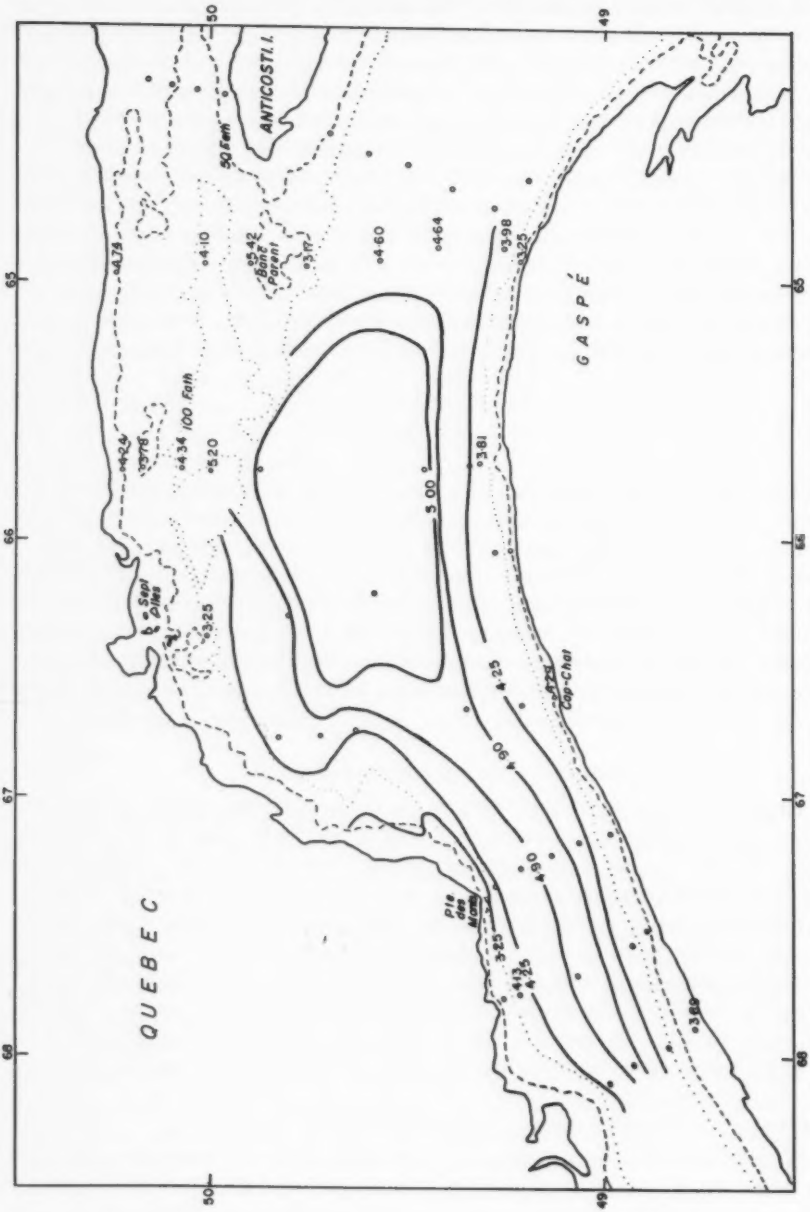

FIG. 2. Regional distribution of Fe contents in the St. Lawrence estuary. Values contoured in the Laurentian trough; representative values given for other areas.

TABLE I. Total Al, Fe, Mn, and Ti contents (% except ppm for Mn), and element ratios in various size-fractions of three representative sediments.[a,b]

Station[c]	Element	>50 μ (sand)	50–37 μ (silt)	37–16 μ	16–2 μ	<2 μ (clay)
50	Al	7.06	7.25	6.80	7.35	7.51
63	"	6.95	6.43	6.96	7.72	7.76
69	"	6.84	8.23	7.99	7.51	7.89
50	Fe	2.75	2.90	3.76	4.77	5.14
63	"	3.29	3.40	4.11	4.80	5.58
69	"	2.18	3.05	4.13	4.78	5.71
50	Mn	426	542	643	666	674
63	"	674	875	829	1007	1022
69	"	500	449	426	759	805
50	Ti	0.29	0.37	0.56	0.49	0.40
63	"	0.35	0.34	0.53	0.41	0.41
69	"	0.28	0.36	0.55	0.45	0.43
		Element ratios				
50	Fe/Al	0.39	0.40	0.55	0.65	0.68
63	"	0.47	0.53	0.59	0.62	0.72
69	"	0.32	0.37	0.52	0.64	0.72
50	$Mn/Al \times 10^{-1}$	0.060	0.075	0.095	0.091	0.09
63	"	0.097	0.14	0.12	0.13	0.13
69	"	0.077	0.055	0.053	0.10	0.10
50	Mn/Fe	0.015	0.019	0.017	0.014	0.013
63	"	0.020	0.026	0.020	0.021	0.018
69	"	0.023	0.015	0.010	0.016	0.014
50	$Ti/Al \times 10^{-1}$	0.41	0.51	0.82	0.67	0.53
63	"	0.50	0.53	0.76	0.53	0.53
69	"	0.41	0.44	0.69	0.60	0.55

Sand fraction of station 69 subdivided into various fractions (mm)

Element	>1	1.0–0.5	0.5–0.297	0.297–0.053
Al(%)	7.25	7.12	7.13	6.89
Fe(%)	1.52	0.93	1.22	3.38
Mn(ppm)	292	218	241	805
Ti(%)	0.20	0.16	0.14	0.43

[a]Determined by the Rapid Silicate Method (Riley, 1958).

[b]Distinguishing characteristics of the sediments are:

Station	Sediment type	Median diam (μ)	Material <16 μ (%)
50	Protected basin pelite	18	43
63	Central estuary pelite	2.5	88
69	Sandy (30%) pelite	17	42

[c]For locations see Fig. 1.

values given for other areas.

TABLE II. Contributions[a] of the various size-fractions to the total Al, Fe, Mn, and Ti contents[b] of three representative sediments.

Element	>50 μ (sand)	50–37 μ (silt)	37–16 μ	16–2 μ	<2 μ (clay)	Total	
						Calculated	Determined from sample
Station 50; protected basin pelite							
Al	0.79	1.07	2.17	1.77	1.36	7.16	7.21
Fe	0.31	0.43	1.20	1.15	0.93	4.02	4.10
Mn	47.5	80.1	204.9	160.4	122.1	615	581
Ti	0.03	0.055	0.18	0.12	0.072	0.457	0.437
Station 63; deepwater pelite							
Al	0.16	0.022	0.699	3.50	3.26	7.64	7.68
Fe	0.076	0.012	0.41	2.18	2.34	5.02	5.10
Mn	15.6	3.0	83.3	456.6	428.8	987.3	1100
Ti	0.008	0.012	0.053	0.186	0.172	0.431	0.527
Station 69; sandy pelite							
Al	2.08	0.27	1.39	2.07	1.69	7.50	7.32
Fe	0.66	0.099	0.72	1.32	1.22	4.02	4.29
Mn	152.1	14.6	73.9	209.6	171.9	622.1	660
Ti	0.086	0.012	0.095	0.124	0.092	0.409	0.419

[a]Determined by Rapid Silicate Method (Riley, 1958).
[b]Total element content (% except ppm for Mn) of size-fraction × percentage by weight of that fraction in the sediment.

Fe or "free" iron makes up 3–16% of the total iron (Table III). These results show that most of the iron is insoluble and that the concentration of "free" iron is highest in pelites from the central trough whereas bank and slope sediments have lower concentrations.

Hydroxylamine–Hydrochloride Soluble Fraction

Much smaller amounts of iron (0.2–0.9% of the total) were dissolved by hydroxylamine–hydrochloride and the amounts do not appear to be related to sediment texture (Table III).

Geochemical Significance

Total Fe and Fe^{+3}/Fe^{+2} values are similar (Table IV) to those of Canadian and other continental shield rocks (Grout, 1938; Poldervaart, 1955). Similar total Fe concentrations are also found in Norwegian glacial clays (Goldschmidt, 1933) and Antarctic glacial marine sediments (Angino, 1966). Intermediate and mafic igneous rocks (Nockolds, 1954) and deepsea sediments (Turekian and Wedepohl, 1961) have greater Fe concentrations but those of granodiorites and quartzofeldspathic gneisses are lower (Poldervaart, 1955) presumably because of source rock differences and differences between the deposition conditions for deepsea clays and the St. Lawrence sediments. The similarity of the Fe contents of St. Lawrence sediments and Canadian Shield rocks indicates that most of the iron-bearing silicate minerals were derived from the Canadian Shield. Nota and Loring (1964) found that most sediments in the estuary were produced by glacial erosion or by reworking of glacial deposits. Mechanical erosion has rapidly reduced the particle size so that little chemical weathering has taken place during transportation and deposition. Therefore, the close relationship between the chemical–mineralogical composition of the sediments and that of their source rocks might be expected.

Most of the iron is structurally combined in the lattice of the silicate minerals and in resistant iron oxides (Table III). In the sand grade, iron as well as manganese is relatively enriched in the 0.297–0.05 mm fraction (Table I). This coincides with the predominant size range of heavy minerals. The most likely host minerals of iron are the silicates: ilmenite, magnetite, and pyrite. These primary minerals are also present in the silt and clay size-fractions. In addition, there is also iron in the clay mineral lattices, probably substituting for Mg^{+2} and Al^{+3}.

The physical processes of transport and deposition of iron-bearing detrital minerals are well known. However, the effect of the physicochemical environment is difficult to assess because changes in environment and iron in solution must also be considered.

Some enrichment of the fine grained sediments with iron is indicated by the increasing Fe/Al ratios with decreasing grain size in the estuary as well as in the individual size-fractions (Table I). Iron is concentrated in the <16 μ size-fraction of these sediments, e.g. station 63 (Table II), and a small but

TABLE III. Partition of Fe and Mn in the dithionite and hydroxylamine–HCl soluble phases of sediments.

Station	Location	Lithology	Median diam (μ)	Total Fe (%)	% of total soluble		Total Mn (*ppm*)	% of total soluble in hydrox-HCl
					In dithionite	In hydrox-HCl		
54	Protected basin	Protected basin pelite	15	4.48	9.5	.26	650	4.5
55	Bank	Sandy pelite	50	5.20	10.1	.44	635	6.5
56	Central trough	Deepwater pelite	3	5.26	15.3	.47	2672	59.6
57		Deepwater pelite	1	5.02	15.9	.20	1247	48.1
58	Slope	Sandy pelite	10	4.41	3.2	.63	612	9.4
59		Sandy pelite	40	3.81	11.5	.86	883	6.8

TABLE IV. Comparison of average Fe, Mn, and Ti contents (%) and element ratios for the St. Lawrence sediments with those reported for rocks and sediments from other areas.

	Fe[a]	Fe^{+3}	Fe^{+2}	Mn	Ti	Fe/Al	Fe^{+3}/Fe^{+2}	$Mn/Fe \times 10^{-1}$	Al_2O_3/TiO_2
Continental shield crystalline rocks (Poldervaart, 1955)	3.46	1.26	2.18	770	0.36	0.34	0.56	0.22	26
Granodiorites (Nockolds, 1954)	2.94	0.91	2.02	770	0.36	0.42	–	0.26	–
Intermediate igneous rocks (Nockolds, 1954, p. 1032)	6.70	2.31	4.05	1540	0.90	0.61	0.58	0.23	11.2
637 Mafic igneous rocks (Nockolds, 1954, p. 1032)	8.25	1.89	6.30	1540	1.30	0.81	0.29	0.18	11.2
Canadian shield rocks (Grout, 1938)	3.98	1.66	2.27	560	0.48	0.45	0.74	0.14	20.3
250 quartzofeldspathic gneisses (Poldervaart, 1955)	2.68	1.12	1.15	770	0.36	0.42	0.72	0.29	29
Glacial and post glacial Norwegian clays (Goldschmidt, 1933, p. 124)	5.10	–	–	–	0.48	0.59	–	–	20.5
Deepsea sediments (Turekian and Wedepohl, 1961)	6.50	–	–	6700	0.46	0.80	–	0.98	–
Antarctic glacial marine sediments (Angino, 1966)	3.72	–	–	1401	0.36	0.51	–	0.37	22.4
St. Lawrence sediments (avg of 50)	4.24	1.59	2.16	720	0.40	0.57	0.74	0.17	21.2

[a]Total Fe as Fe_2O_3.

significant proportion of the total iron is also held in amorphous iron compounds, in oxides, or in sorbed positions on clays (Table III). This could be the result of oxidation of undecomposed detrital material at the sediment–water interface; or it may have formed as iron oxide coatings on suspended matter (Carrol, 1958) or have been deposited from solution. Eisma et al. (1966) found that on the Dutch Coast significant quantities of iron have precipitated, but in the Gulf of St. Lawrence no evidence for this was found.

Most of the silt and clay ($<16\ \mu$) in the trough has been deposited from suspension after thorough mixing in well-oxygenated water (Nota and Loring, 1964). This would have provided ample opportunity for the formation of iron oxide coatings. After deposition the retention of iron in this state and the formation of additional oxides depend on the length of time the material remained in contact with the oxygenated bottom waters before it was buried. Evidently, only about 16% of the total iron can be retained as an iron oxide film at the sediment–water interface with the present rate of sedimentation (22 cm/century, Nota and Loring, 1964).

MANGANESE

Abundance and Distribution

Manganese contents of the estuary sediments (Fig. 3) vary between 433 and 2672 ppm with an average value of 720 ppm. The regional distribution pattern is similar to that of Fe. Lowest concentrations are in the sands and sandy pelites of the nearshore and bank areas, and higher concentrations are in the deepwater pelites from the central part of the submarine trough. In any one sediment, concentration of Mn generally increases with the decreasing grain size of individual size-fractions (Table I). This accounts for the relationship between Mn content and sediment texture (Table II).

Chemical Partition of Mn in the Sediments

Hydroxylamine–hydrochloride Mn accounts for 5–60% of the total manganese which varies with sediment texture and location (Table III). Highest values occur in the deepwater pelites and lowest values in the bank, slope, and protected basin pelites. These results indicate that a considerable proportion of the soluble Mn in pelites is either in the form of reducible Mn oxides or is held in sorbed positions.

Relation between Manganese and Iron

The close geochemical coherence of Mn and Fe is well known and has been studied extensively in rocks and sediments of all kinds (Krauskopf, 1957). In the estuary, manganese varies sympathetically with iron and both vary with sediment texture. Lower Mn/Fe ratios occur in the coarser grained inshore sediments, whereas higher ratios are found in the pelites occupying the central part of the trough (Fig. 4). In any one sediment the Mn/Fe ratios decrease slightly with decreasing grain size of the individual size-fractions

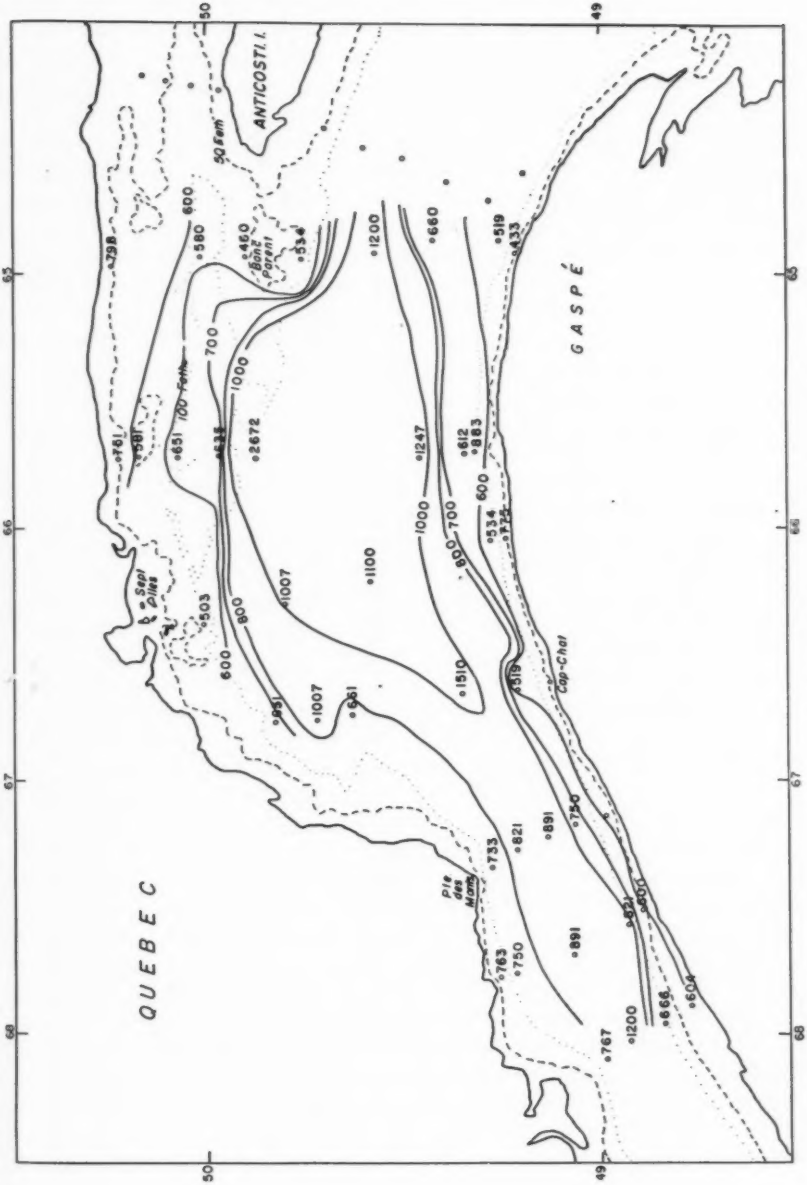

FIG. 3. Regional distribution of Mn contents.

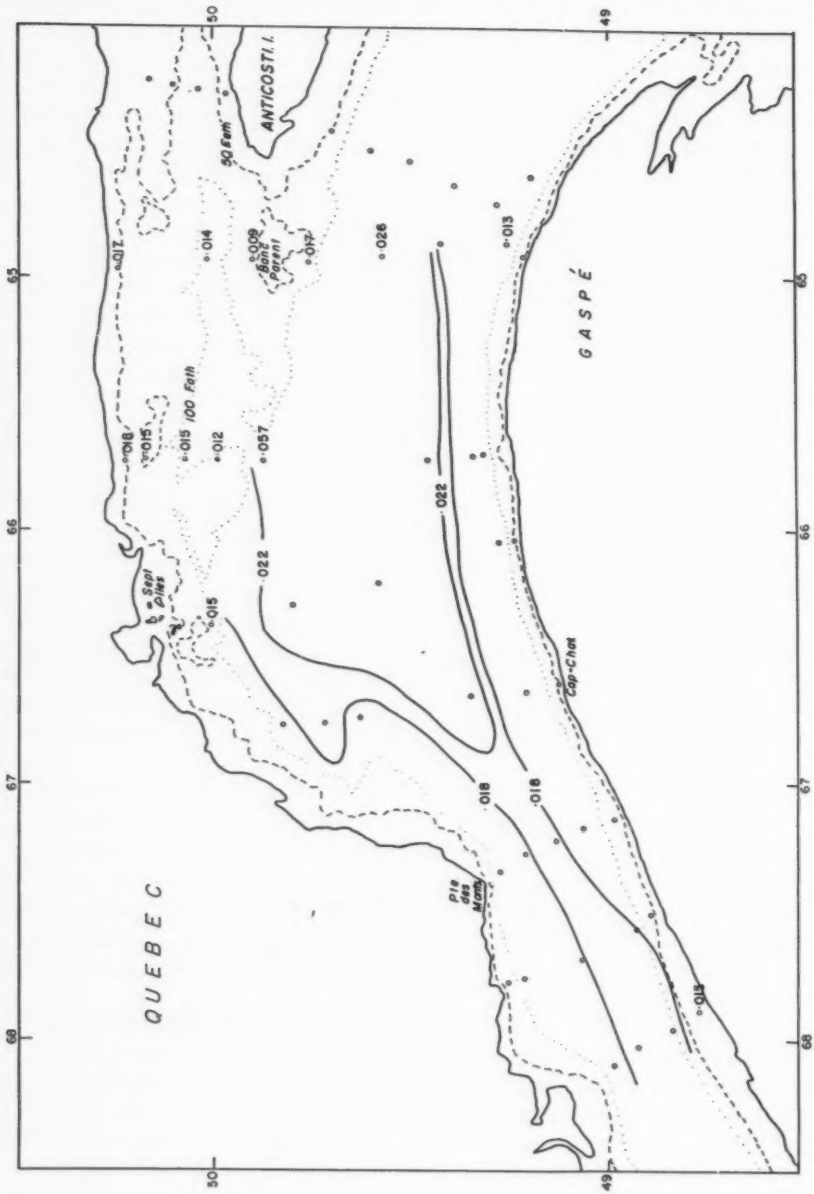

FIG. 4. Regional variation in Mn/Fe ratios.

(Table I). This indicates a slight preferential enrichment of the sand and the coarse silt fractions of the pelites with manganese-bearing minerals. The enrichment of the deepwater pelites with Mn relative to Fe is evidently due to high Mn/Fe ratios of their fine fractions (Table I). There is also some enrichment of the soluble phase of the sediment with Mn in relation to Fe. The Mn/Fe ratios of the soluble fractions (hydrox-HCl/dithionite) vary between 0.008 and 0.19. In the deepwater pelite samples (stations 56–57), the high Mn/Fe ratios (0.07–0.19) indicate that there is an appreciable enrichment with soluble Mn in relation to Fe. This suggests that differences in the level of the Mn/Fe ratios between the deepwater pelites and the other sediments are due to differences in the amounts of soluble Mn held by them (Table III).

Geochemical Significance

The average amount of Mn in the St. Lawrence sediments is similar (Table IV) to that in continental crystalline shield rocks (Poldervaart, 1955). granodiorites (Nockolds, 1954), and quartzofeldspathic gneisses (Poldervaart, 1955). However, the Mn is much less than that of Antarctic glacial marine sediments (Angino, 1966) because of source rock differences, and that of deepsea sediments because of differences in source and depositional conditions. Since the average Mn/Fe ratio of the St. Lawrence sediments is slightly higher than that of the Canadian Shield rocks, it is evident that the sediments have become slightly enriched with Mn in relation to iron during weathering, transportation, and deposition. However, the St. Lawrence sediments are not as rich in Mn in relation to Fe as are glacial marine sediments of the Antarctic Shelf or deepsea clays. Consequently, they cannot be regarded as being rich in Mn with respect to their source rocks. Nor are they especially enriched with Mn in relation to iron.

Between 90 and 94% of the total manganese in the shallower water pelites is held in detrital minerals and in clay minerals as a replacement ion. The detrital minerals are: hornblende, augite, hypersthene, biotite, calcic-feldspars, detrital iron ores, and insoluble Mn oxides. However, Mn found in the soluble fraction accounts for its enrichment of the deepwater pelites. In the deepwater pelites only 40–52% of the Mn is detrital. The rest of the Mn in these sediments occurs mainly in the fine fraction ($<16\ \mu$) either in sorbed positions in clays or as soluble Mn oxides. This can be inferred from the interrelationships of Mn content, mineralogy, and grain size (Table I). Both Mn content and Mn/Al ratios generally increase as grain sizes decrease, but in the material $<16\ \mu$ they remain relatively constant.

Although the pathways by which the detrital host minerals of Mn have entered the estuary are fairly clear, the precise mechanisms involved in the incorporation of manganese into the soluble phase of the sediments (Goldschmidt, 1954, p. 632–638; Krauskopf, 1957) are not so easily established. Soluble Mn may have been incorporated into the sediments in a number of ways. The two basic mechanisms are: incorporation of dissolved manganese at the

oxidized sediment–water interface of the deepwater pelites, and modification of detrital Mn-bearing host minerals during transportation and deposition.

Manganese in deepsea clays is believed to be derived from solution, in conjunction with the iron colloid aquate deposited at the sediment–water interface. Iron aquate forms a highly active surface which catalyses the oxidation of dissolved manganous ions. This in time combines to form ferric manganite. The amount of Mn accumulating depends on the length of time that the active interface is exposed to sea water (i.e., rate of sedimentation), and to the rate of supply of ferric oxides (Goldberg and Arrhenius, 1958). In the estuary some Mn may be incorporated into the sediments from solution, but the relatively high rate of sedimentation of the pelites may limit the amount of Mn which can be incorporated in this way. Studies by Manheim (1965) in the Gulf of Maine indicate that Mn is removed from sea water and encrusted onto pebbles and sand grains only in areas swept clean of fine detritus. In the St. Lawrence estuary there is little chemical evidence to suggest that Mn has become incorporated at the interface.

The other basic mechanism involves the derivation of soluble Mn from the chemical modification of detrital minerals during transportation and deposition. Groot (1964) has shown that the amount of Mn in the detrital material is dependent on its source. He postulated that during transportation in oxygenated waters detrital minerals cannot lose Mn because it is nearly all structurally combined or present as insoluble oxides. After deposition, however, reduction can take place (with the loss of exchangeable Mn). The presence of relatively large amounts of soluble Mn in the deepwater pelites of the St. Lawrence estuary may be due to a similar mechanism. Most of the particles $<16\ \mu$ have been recently deposited from suspension after thorough mixing (Nota and Loring, 1964). This would insure that any Mn associated with the suspended matter would be retained, and would also provide an opportunity for additional Mn to be transferred from solution to the surface of the suspended matter. After deposition, Mn would probably be retained in a higher oxidized state at the sediment–water interface, but after burial it would be reduced to the mobile, exchangeable form.

Since the degree of reducibility is related primarily to the degree of crystallinity, the freshly deposited Mn oxides (less crystalline) are evidently reduced easily. The predominance of ferrous iron below the sediment–water interface would also encourage reduction of Mn to more mobile forms. Groot (1963) showed that Mn is more easily reduced than Fe^{+2} and that ferrous ions are able to enhance the reduction of Mn.

Modification of Mn-bearing suspended material occurs, therefore, during transportation and deposition, and also after deposition.

In addition, slight differences in the sources of suspended material for the deepwater pelites and protected basinal pelites are suggested by their differences in the total Mn content of the material $<16\ \mu$. Differences in rates of sedimentation or age between the deepwater pelites and the protected basinal pelites may also be inferred from differences in the amounts of soluble

Mn held by them. Essentially, it seems that the behaviour of Mn is determined not only by its detrital host minerals but also by the physicochemical environment.

TITANIUM

Unlike iron and manganese, titanium is not affected by the physicochemical conditions. It behaves like the other major elements such as Al, Na, and K in the estuary (cf. Nota and Loring, 1964, p. 225–232).

Titanium contents vary from 0.31 to 0.64% (Fig. 5) with an average value of 0.40%. The deepwater pelites tend to contain slightly more Ti than the nearshore sediments. Extremely high values are, however, found in several of the more sandy bank sediments from the north shore. There is a slight increase in Ti content with decreasing grain size of individual size-fractions only to the 37–16 μ fraction (Table I). The relatively small amount of this fraction in the deepwater pelites and the correspondingly high content of material >16 μ accounts for the relatively high Ti values in these sediments (Table II).

Geochemical Significance

The St. Lawrence sediments have Ti contents similar to those of average crystalline shield rocks, granodiorites, quartzofeldspathic gneisses, and Canadian Shield rocks, but much lower contents than intermediate and mafic igneous rocks (Table IV). The average Al_2O_3/TiO_2 ratio is similar to those of Canadian Shield rocks and Antartic glacial marine sediments, but is much higher than those of the intermediate and mafic igneous rocks. Since the abundance of Ti, both absolutely and relative to the aluminosilicates, is almost the same as in the Canadian Shield rocks, there is little indication of any increase in or depletion of Ti during weathering, transportation, and deposition. This reflects in turn the association of Ti with detrital minerals derived from the Canadian Shield.

In the sand fraction Ti occurs as titanite, and also as a trace constituent in the ferro–magnesium minerals. Some Ti may also be located in the opaque minerals (e.g., ilmenite). In the silt and clay fractions, Ti is located in minerals similar to those contributing Ti to the coarser fractions, although some may be present as trace constituents in the clay minerals.

Most of the Ti in the sediments is detrital. Within the estuary, Ti follows Al fairly closely despite marked changes in grain size. This indicates that Ti accumulates at the same rate as detrital sedimentary material. However, Ti is concentrated relative to Al in the 37–16 μ fraction, showing an enrichment by detrital Ti-bearing minerals (Table II). The finer silt fractions are characteristically enriched in detrital minerals such as rutile (Van Andel, 1959). Goldschmidt (1954, p. 429) has suggested that very little Ti is chemically or physically bonded to clay minerals and the Ti of clays is probably present as very finely crystalline TiO_2. Thus, it appears that Ti enters the sediments of the estuary in detrital host minerals and its distribution pattern is a reflection

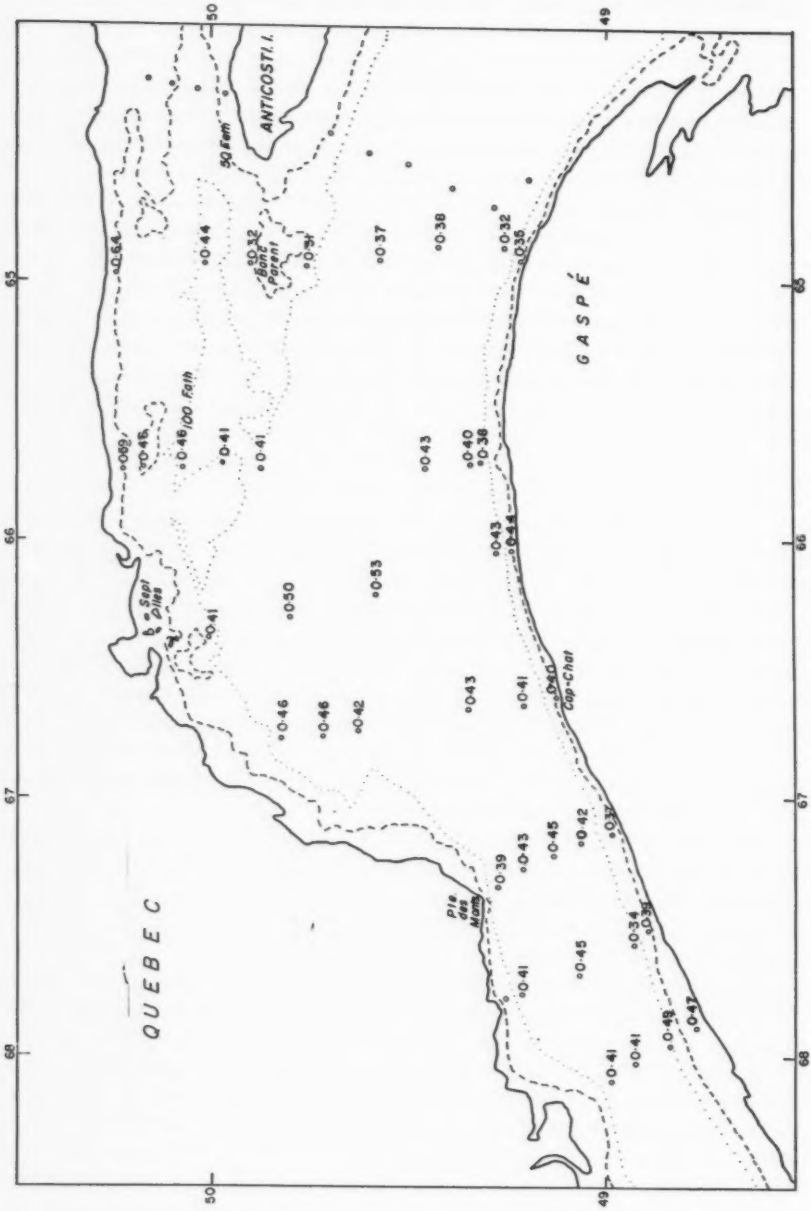

FIG. 5. Regional distribution of Ti contents.

of the abundance and characteristic grain size of these host minerals and of the physical conditions of sedimentation. The high concentration of Ti in shallow water sediments from the north shore is due to the close proximity of Ti-bearing source rocks.

CONCLUSIONS

In the sediments of the St. Lawrence estuary, iron, manganese, and titanium are not greatly enriched or depleted in comparison with the probable source rocks. However, their geochemistry is determined not only by detrital minerals, which are hosts of these elements, but also by the physicochemical environment.

Most of the iron is in the ferrous state, and has entered the depositional basin structurally combined in detrital silicate minerals and as detrital iron ores. Small but significant amounts of iron, however, have entered the basin as oxide films on suspended matter, and some may have been transported in solution. The abundance and distribution of "free" iron is determined by the nature and rate of deposition of suspended matter. It is also determined by the positive oxidation potential in the water and at the sediment–water interface and by the negative potential below the sediment–water interface. In general this iron is present as oxide coatings on suspended matter. Some of this was present originally and some has been formed by the modification of detrital minerals in the estuary. Additional iron may have been formed by sorption from solution both in the water and at the sediment–water interface. Below the interface, the oxide coatings are reduced. The iron is mobilized but is still strongly held in the sediments.

The geochemistry of manganese is determined by primary and secondary oxide minerals. The latter have become associated with detrital minerals either at their source or during transportation and deposition. Primary detrital silicate minerals are an important source of manganese in some of the sediments, but a large part of the Mn, especially in the deepwater pelites, has entered the basin as oxide films on suspended matter. In general, Mn oxide films are retained on the suspended matter in the oxygenated waters of the estuary and at the sediment–water interface. Below the interface, Mn is mobilized in the reduced state. The relatively rapid sedimentation rate appears to have prevented the accumulation of high concentrations of manganese, which would lead to the formation of manganese or ferro–manganese nodules. Conditions favorable for the extraction of Mn from sea water seem to be present on the banks, where sedimentation rates are much lower, but no Mn-coated pebbles or coarse sand grains were observed. The abundance and distribution of titanium in these sediments is determined by the abundance, distribution, and characteristic size range of detrital Ti-bearing minerals. There is no evidence to suggest that any Ti has entered the depositional basin in solution.

This investigation clearly shows that despite the derivation of sedimentary material from the Canadian Shield by predominantly nonchemical erosional

FIG. 5. Regional distribution of Ti contents.

processes, small but significant chemical modification of iron- and manganese-bearing material is taking place in the estuary in response to present physicochemical conditions.

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Direct Estimation of a Fish Population Acoustically[1]

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ABSTRACT

A method is described of estimating fish stocks by length-groups acoustically. Hake off southern Africa were recorded as individuals on the paper record of a Kelvin Hughes "Humber" echo sounder down to 350 fath. Signal strengths of single fishes were observed on the cathode ray tube and the target strengths of fishes are known; estimates of fish sizes were made. The signals were considered as being received from a mean angle (to the axis of transmission) in the volume insonified. Hence, average target strengths, average numbers/unit volume, and average heights above the sea bed were calculated.

The echo survey made between Cape Town and Walvis Bay was expressed as numbers of fish/unit volume in a range gate of 1 or 4 fath above the sea bed. A length distribution of the hake stock was derived.

RÉSUMÉ

On décrit une méthode pour estimer les stocks de poissons par groupes de longueur avec l'aide d'un écho-sondeur. Des merlus de la côte d'Afrique du Sud ont été enregistrés individuellement sur le papier enregistreur d'un écho-sondeur du type Kelvin Hughes "Humber" jusqu'aux profondeurs de 350 brasses. L'amplitude des signaux provenant de chaque poisson était observé sur l'écran cathodique et les "target strengths" étant déjà connus on peut donc estimer la taille individuelle des poissons. Les signaux on été considérés comme s'ils étaient reçus d'un angle moyen (moyen à l'axe d'émission) dans le volume exploré par le faisceau. Donc les amplitudes moyennes de réception, le nombre moyen de poissons/unité de volume et les hauteurs moyennes des poissons au-dessus du fond étaient calculés.

Les résultats du relevé acoustique fait entre Cape Town et Walvis Bay sont exprimés en nombre de poissons/unité de volume dans un intervalle de 1 ou 4 brasses au-dessus du fond de la mer. On a calculé la répartition des longueurs des merlus dans le stock.

INTRODUCTION

Before fish can be sized and counted acoustically there are three preliminary requirements: that they be identifiable, be recorded as individuals, and that the echo sounder be calibrated. The identification of fishes by acoustic means is possible but not yet practicable. It will be shown below that an estimate of size can be made from the signal received from a single fish. But this is not identification. Satisfactory identification is achieved only by capture; but given that capture is adequate, then the identification is that of the proportions caught. Between points of capture, the information is interpolated. Then a few hauls confirming the identification endows an echo survey with the sampling power of a commercial fleet. If the proportions of different species

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vary randomly between hauls, the stocks must be very small ones, but the estimates of numbers of single fish will be valid as numbers of "fish" by length-groups.

To count fish by size-groups, a method is needed for recording fish as individuals. The commercial echo sounder records fish sometimes as individuals and sometimes in shoals. A signal from a single fish is easily recognized because, as it is repeated, it is never longer than one pulse length. Further, with trace-to-trace correlation, the typical fish trace has a recognizable character. Trout et al. (1952) showed that tagged cod released from a research vessel could be followed on the echo-sounder record all the way down to 60 fath where they joined a layer. The layer was composed of traces also of minimum pulse length and so it was also composed of single fish.

Saetersdal and Hylen (1959) made extensive echo surveys in the Barents Sea in spring and autumn. Cod were identified as being large single fish in mid water. It was a special case in that cod are the only large fish in the deep water of the Barents Sea, but it drew attention to the possibility of counting fish as individuals. Technically the problems are to reduce the angular resolution and the range resolution. By transmitting at a higher frequency (100–500 kHz), narrow beam angles (1–10°) and shorter pulse lengths (20–100 μsec) can be readily obtained. It is now possible to resolve single sprats and herring, at least at night, with the Lowestoft 100 kHz equipment. The disadvantage of high frequency is that attenuation increases with frequency and so greater power is needed to attain useful ranges.

The Kelvin Hughes "Humber" equipment obtains high resolution in another way. It transmits at 30 kHz and it has a fairly narrow beam angle (9° × 14°, to the first minima in echo), a pulse length of 0.25 msec, and an output of 8 kw of electrical power into the transducer (a sound pressure of 128.9 db ref 1 μbar). The bottom echo is locked at a fixed point on the paper chart and on the CRT, and the 4-fath zone above the bottom appears on a presentation 6 inches wide. With very high-speed recording and very fast paper speeds, the signals from hake or cod are resolved into individual fish traces at depths as great as 350 fath.

There are thus two ways of resolving signals from single fishes. The first is with high frequency, with high resolution in angle and in range; the second is with very high-speed recording and very high power output in deep water. Here fish are large and relatively far apart, and they can be resolved by high-speed recording.

Before sizes and densities of single fish signals can be estimated, the echo-sounder system should be standardized. This means that the source level (or transmitted power) should be maintained, preferably from an outboard transducer, to avoid the ship's bubble layer. The calibration can be monitored electrically by measuring the input of electrical energy to the transducer or acoustically by measuring its acoustic output. The amplifier should also be monitored with signals injected into the receiver line from the transducer. The same method is used to measure reverberation, when transmitting, or

water noise, when not transmitting. The total noise level, the sum of water noise and reverberation, is needed to estimate the range of the echo sounder. With a constant source level or power output, the maximum range at which a fish of a given size can be detected varies with noise level, which changes from ship to ship, under different weather conditions, and in different depths of water. But with a transducer of constant source level (in db ref 1 μbar), the signal received from a fish of given size at a determined position remains the same. The chance of detection is estimated in the signal-to-noise ratio. If noise level is low and signal-to-noise ratio is high, the signal is presented unequivocally for measurement. So the maximum range for a fish of given size, and hence the volume in which it can be detected, or sampling volume, is limited by the noise level. But within that sampling volume, the signal from a fish of a given size is predictable, if the source level is known.

The requirements before estimating absolute numbers of a fish stock are threefold. First the fish are identified by capture and therefore the enumeration should be limited to the depth zone in which the capturing gear is effective. Secondly, the fish are recorded on paper or in an electronic store as individuals and so can be counted per unit time or distance in the depth zone as delimited by the capturing gear. Thirdly, the transducer should be calibrated and the amplifier monitored, so that the signals from the individual fish can be assigned to size-groups and to sampling volumes.

THE TARGET STRENGTH OF FISHES

The target strength of a fish of given size is defined within the sonar equation, which can be written as:

$$E = S + T - 2H \qquad \ldots\ldots(1)$$

where S is the source level of the transducer; H is the one-way propagation loss, comprising spreading and attenuation ($H = a.r + 20 \log r$, where a is the attenuation coefficient and r is the range in yards); T is the target strength of a single fish of a given size; E is the observed echo level or signal strength. Measurements of source level are made in db ref 1 μbar. The measure of target strength is dimensionless.

The target strength of fish is expressed as at unit distance from the transducer. There are two relations of interest, the dependence of target strength on length of fish, at one frequency, and the dependence of target strength on frequency for fish of the same length. The dependence of target strength on length of fish is given in Fig. 1, showing the relation given in Cushing (1964), based on the measurements of Midttun and Hoff (1962), Cushing et al. (1963), and Harden Jones and Pearce (1958). Target strength increases as a power of the length of between 2 and 3, more nearly 3. This is unexpected because one would expect the energy to be scattered roughly as the cross-sectional area. It is possible that (as Midttun and Hoff suggest) a component of directivity from the air bladder comes into the calculation.

The dependence of target strength on frequency is complicated by the fact that fish sizes at most of the frequencies used tend to lie between the zone of Rayleigh scattering and that of specular reflection. Hashimoto and Maniwa (1956) have shown that the target strength increases slightly with frequency:

Frequency (*kHz*)	Target strength (*db*)
28	–48
100	–42
200	–39
400	–36

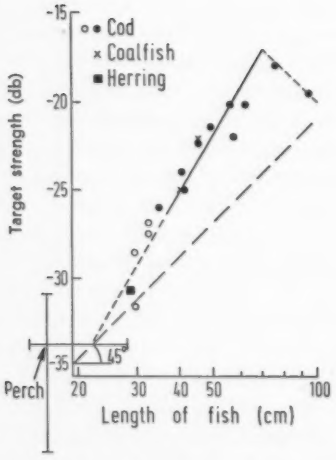

FIG. 1. The dependence of target strength (in db) upon length of fish (Cushing, 1964, from the data of Midttun and Hoff, 1962, Cushing et al., 1963, and Harden Jones and Pearce, 1958).

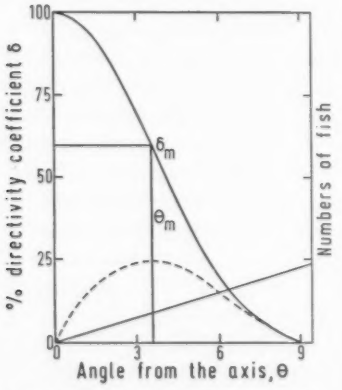

FIG. 2. The mean angle, θ_m, from which signals are received on average at a given range. The directivity coefficient, δ, is shown as a function of the angle from the axis of transmission, θ. The right-hand ordinate shows the increase in numbers of fish with $(\tan \theta)^2$. The broken line shows the product distribution of signal from numbers of fish. The mean angle, θ_m, is the mean of the product distribution.

Sardines and horse mackerel were used in these experiments. It will be seen that the reflection loss decreases by 12 db for an increase of just over 14 times in frequency.

Thus, given range and frequency, the size of an individual fish can be specified from the signal strength as received at any range.

THE STATISTICS OF RECEIVED SIGNALS

The signals received from single fish come from any part of the sound cone; because of the great differences in directivity, there is considerable

variation in signal from any particular range. The signal from each fish is transient, being received for a small number of transmissions. The fish crosses the sound cone along a chord track, shortening the range until it reaches the midpoint of the chord and then extending it again. Hence the trend of signal in time for a single fish is a systematic one. An average signal strength must be based on measurements made on many signals, enough to randomize the systematic trend and enough to establish the mean. The mean voltage and mean height above the bottom can be estimated in this way.

From the axis of transmission, the directivity coefficient decreases sharply with θ, the beam angle of the transducer. Figure 2 shows the distribution of directivity in angle θ. It also shows the distribution of fish in angle θ, the numbers increasing as the square of the angle for angles less than 20°. To simplify, let the volume insonified be a cone of height r_1 with base of radius r' and apex angle 2θ. Numbers of fish on the base of the cone increase as the square of the radius (i.e. $n = kr'^2$, where n is the number of fish and k a constant). Also $r' = r_1 \tan \theta$, and so $\tan \theta = \frac{1}{r_1}\sqrt{\frac{n}{k}}$. There are two distributions, that of directivity decreasing with the angle θ and that of fish numbers increasing with the angle θ. The product distribution peaks at a middle angle, θ_m, at which the directivity coefficient is δ_m. The mean angle, θ_m, is the point, at a given range, from which the average signal voltage is received. The variance of the product distribution is complex.

The mean angle, θ_m, is constant at short and middle ranges. At maximum range, the signal from a fish of a given size is received on the axis only. So there is an intermediate point in range beyond which θ_m tends towards zero and δ_m tends towards unity, reaching it at maximum range. The intermediate point in range, r_z, is defined: $r_z^{\frac{1}{2}} = r_{\max}^{\frac{1}{2}} \cdot \delta_{\min}$, where $r_{\max}$ is the maximum range and $\delta_{\min}$ is the directivity coefficient at which the signal reaches a conventional ratio to the noise level, near the first minimum at $\theta_{\min}$. The convention is necessary because at $\theta_{\min}$ the signal received in echo should be zero. As the point of maximum range, $r_{\max}$, must be on the axis, the signal is calculable for any size of fish, if its target strength is known. So the mean angle, θ_m, can be calculated at all ranges between r_z and $r_{\max}$.

Thus, between the transducer and the maximum range for a fish of given size, the mean angle, θ_m, is calculable throughout the sampling volume, the volume within which a target of given size can be detected, conditions of noise being known. For each size of fish, there is a specific sampling volume, a maximum range and a mean angle, θ_m, at each range. So long as the signals from single fish are properly averaged, it becomes possible to make good estimates of size.

When the average height of fish above the bottom is considered, the distribution of fish of different sizes in the volume sampled must be taken into account. The volume sampled in a period of time is a set of shells overlapping in the direction of the ship's track. To simplify, consider an anchored

ship and the fish crossing the volume sampled, their tracks making chords across the spherical shell. If the fish are of different sizes, the lengths of the chords depend upon the target strength of the fishes. Consequently, the distributions in Fig. 2 apply to the repeated transmissions from an anchored ship, and the average chord or fish track passes through θ_m. The same argument applies if the volume sampled is a set of overlapping shells formed from a moving ship. Thus, the special case of the height of fish off the bottom can be calculated in the same way, as the height above the bottom at the mean angle, θ_m (Fig. 3).

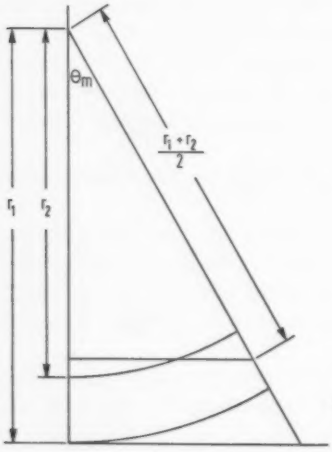

FIG. 3. The mean height of fish above the bottom, as estimated at the mean angle, θ_m.

THE ESTIMATION OF FISH SIZES

The dependence of target strength on size of fish in Fig. 1 implies that sizes can be estimated from observed signal strengths. If they are adequately averaged, the voltages are considered as being received from the mean angle at any given range. Further, theoretical curves of signal strength on range in any units can be drawn as $T.r^{-2}.\delta_m$ for fishes of given sizes.

Figure 4 shows the theoretical curves of signal strength on range for fishes from 20 to 90 cm long. They are calculated for a Kelvin Hughes Humber gear which has a source level of 128.9 db ref 1 μbar. The directivity coefficient, δ_m, is calculated between the ranges r_z and r_{max} as described in the previous section. The noise level in deep water was 1–5 μv, possibly rising to higher levels in shallow water; accidentally, most observations of noise level were made between 150 and 350 fath. The calculated curve for fish of 20 cm long reaches 5 μv between 200 and 250 fath. If the noise in good weather was 1 μv, the signal-to-noise ratio of a factor of 5 is sufficient to establish a maximum range, for a 20-cm fish, of 200–250 fath. As noise increases, the maximum range obviously decreases if the same signal-to-noise ratio is maintained.

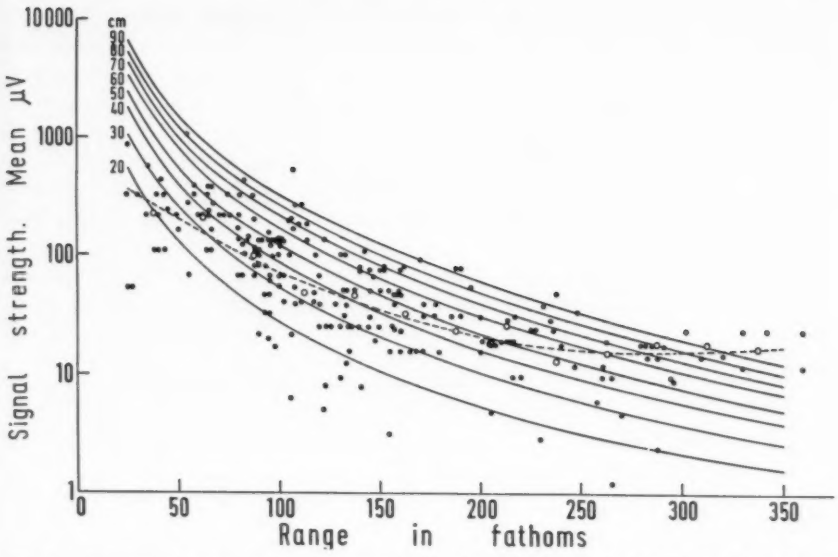

FIG. 4. Theoretical curves of signal strength ($T.r^{-2}.\delta_m$) on range for fishes from 20 to 90 cm long. The points were observed on single fish within a fathom of the bottom off South Africa. The dotted line shows the trend of mean signal with depth, showing that from 20 to 90 cm bigger fish are found in deeper water. The point in 210 fath between the theoretical curves for 40 and 50 cm represents the mean length of catches of hake made by trawlers during the survey.

The points on Fig. 4 were observed on echo survey for demersal fish on the South African continental shelf between Cape Town and Walvis Bay, during a cruise of HMS *Hecla* in February 1966. They were observed as averaged signals received from single fish shown on the A-scan of the CRT. The points are scattered across the grid of theoretical curves, indicating that the sizes of single fish observed lay between 20 and 90 cm. The dotted line represents the mean signal received from single fish at intervals of 25 fath. The small fish of 20 cm live in 25 fath and the biggest fish live in 300–350 fath, a clear demonstration of Heincke's Law (Heincke, 1913). The range in length of 20–90 cm is the range of hake caught by the trawl in the area surveyed. There is a big black circle at a range of 210 fath between the calculated lines for fishes of 40 and 50 cm; it represents the mean length of fish caught by hake trawlers in the area during the period of the survey. The point lies very close to the line of mean observed signal. Hence, it is likely that the echo sounder was roughly sampling the same range of sizes as the trawl. This is reasonable if the noise level lies near the lowest points on a curve parallel to that for the fish of 20 cm long. Figure 4 shows that fish can be sized reasonably well acoustically.

So far the question of identification of the single fish has been left open. The evidence that the fish were nearly all hake is as follows. The mean height of fish off the bottom in the 0–1-fath scan is 0.75 fath. The headline of a Granton

trawl is probably about 1.5 fath off the bottom at its highest. So most of the fish examined in the 0–1-fath scan were vulnerable to capture by the trawl. For hake, the selection length lies just above 30 cm. It is likely that the echo sounder also selects fish by size, merely by the attenuation of the signal; any selection will vary with depth, but examination of Fig. 4 suggests that fish of 20–30 cm are well sampled. Hake trawlers working in three different areas — off Cape Town, south of the Orange River, and off Lüderitz — caught 95% hake. Hence it is thought that the signals on Fig. 4 represent signals from hake.

Figure 5 shows a similar presentation by Nishimura (1963). The calculated lines ($T.r^{-2}$) of sound pressure (in decibels) are plotted on the logarithm

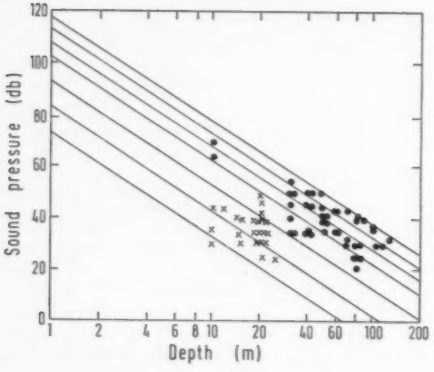

FIG. 5. Theoretical curves of signal strength ($T.r^{-2}$) plotted as decibels on depth in logarithms (Nishimura, 1963).

of depth in metres. The transmitted power was known and so the observed signal at any range can be measured. The observed signals are spread across the grid of theoretical lines, signals from tuna in fairly deep water between 30 and 120 m ranging from 40 to 15 db in "reflection loss" (or $T.r^{-2}$ in db), whereas signals from smaller fish were found in shallower water.

The two presentations in Fig. 4 and 5 are similar. In Fig. 4, the signals were reported in μv, as observed on the CRT. For the Kelvin Hughes Humber gear, the signals at a given gain setting can be converted to decibels, using 1 μbar = 34 db above 1 μv. When sound pressure is expressed in db ref 1 μbar, the signals can be plotted as in Fig. 5 but the lines remain curvilinear. The calculated lines in Fig. 4 were based on a source level of 128.9 db ref 1 μbar, the output of the Kelvin Hughes Humber gear. Those in Fig. 5 were similarly based on the source level of the Japanese echo sounder. The presentation (Fig. 4) is useful at sea when signals are measured on the CRT in μv.

The signals from single fish on the paper record were presented on the cruise off South Africa as recognizable traces (Fig. 6). The scattered single traces, "fingernail" traces (Fig. 6 (*left*)), are recognizable by their hyperbolic character; they are readily counted, but the estimate of average signal strength

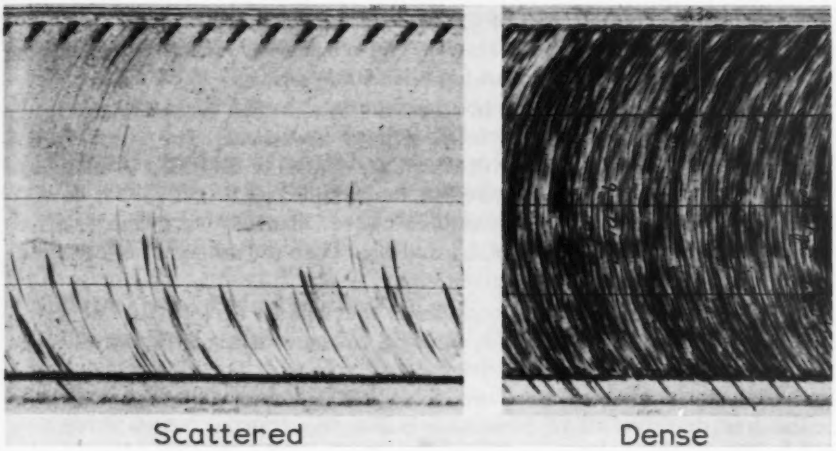

FIG. 6. Single fish recorded by the Triggered Pen Recorder of the Kelvin Hughes Humber gear, showing (*left*) scattered and (*right*) dense traces of single fish.

was made separately. Figure 6 (*right*) shows the case in which counting was still possible, by counting "blobs"; but at any greater density, which occurred infrequently, counting became impossible. Midttun (1966) has described a method of recording continuously the signal strength of discrete signals with a recording microvoltmeter. If the method can be used, a paper record superficially like that in Fig. 6 might be produced continuously, giving the signal strength of each fish detected, and so numbers and sizes are estimated at the same time.

THE ESTIMATION OF FISH DENSITY

An echo survey depends upon the recording of numbers of fish in unit time steamed, which is unit distance. Each fish is recorded in a number of transmissions, necessary for its recognition as a single fish. A single transmission samples a specific volume. The unit time or distance steamed by the research vessel can be split into exclusive volumes sampled. The number of exclusive volumes sampled in unit distance steamed is given by $D/2r.\sin \theta\beta_{min}$, where D is the unit distance in m; r is the range in m; and $\theta\beta_{min}$ is the angle of the minor axis of the transducer ellipse at the first minimum, i.e. in the fore and aft axis. Then the numbers of fish per unit distance can be readily converted to numbers per exclusive volume.

The exclusive volume varies with depth and size of fish. A square transducer examines volumes of $2/3\ \pi\ [r_1^3 - r_2^3]\ (1 - \cos\theta)$, or range shell volumes between r_1 and r_2 in range, where $(r_1 - r_2)$ is the thickness of the shell in m, and θ is measured to the first minimum. For a rectangular transducer the range shell volume is given by $2/3\ \pi\ [r_1^3 - r_2^3]\ [1 - \cos\sqrt{\theta_\alpha \cdot \theta_\beta}]\ m^3$, where θ_α and θ_β are the angles subtended by the major and minor axes of an

ellipse formed as conic section of the beam. This approximation was calculated by my colleague, Mr J. G. K. Harris. The range shell volume is the volume in which a fish of given size can be detected.

Volumes can be calculated in steps of θ, range shell sectors. Each sector is multiplied by the appropriate directivity coefficient. The sum of such weighted sectors gives a volume in which the chance of detection is taken into account. This sum is the effective volume sampled (EVS). From r_z to r_{max}, $\theta_{\alpha m}$ and $\theta_{\beta m}$ are calculable as described above. Similarly $\theta_{\alpha min}$ and $\theta_{\beta min}$ are calculable as fixed proportions of $\theta_{\alpha m}$ and $\theta_{\beta m}$. Then the volumes are calculable from r_0 to r_{max} for a fish of a given size.

So far the treatment has considered the volume sampled in one transmission. During a period of time, the ship covers a distance D and the echo sounder samples a number of overlapping volumes. The fish signal is recognized in two, three, or more successive transmissions, and single fishes are counted in time periods of 10 min or half an hour during which there were 600 or 1800 transmissions.

The total volume sampled by the echo sounder is a set of overlapping shells, each an exclusive volume, on the course on which the ship steams. The appendix to this paper by my colleague, Mr J. G. K. Harris, shows how to estimate the total volume V_T. He also points out that there is an error due to the discontinuity of the repeated signals in time, a downward bias of 6% in 50 fath and 2% in 300 fath. Numbers of fish are counted in unit distance steamed and could then be expressed as numbers per unit volume, V_T. This volume could be weighted by the directivity coefficient in steps of one degree in angle θ_α to allow for the chance of detection.

In the volume sampled by a single transmission, fish are assumed to be randomly distributed about a mean angle and about a mean height above the bottom. The variance of this distribution is complex. In the total volume sampled, V_T, there is effectively a port and starboard mean angle and so the statistical problem is difficult to handle. Lacking a solution, the volume sampled in a single transmission is used to put the statistics on as firm a base as possible and is corrected to the true volume by a series of factors changing with depth.

In Cushing (1968) the error due to treating the volume sampled, V_T, as a series of overlapping exclusive volumes sampled was estimated wrongly as 1.21. In the appendix to the present paper, Harris shows that this error increases with depth from 1.79 in 50 fath to 4.36 in 300 fath. Consequently, in fig. 10 and 11 of Cushing (1968), the densities are overestimated in 125 fath by 2.424 and in 325 fath by 4.497. The same error exists in the length distributions in fig. 12 which are overestimated in the same way. The corrected length distributions are shown in Fig. 7 of the present paper. The corrected estimates of stock are 0.99 M tons in the 0–1-fath scan and 3.36 M tons in the 0–4-fath scan. The 0–1-fath scan represents an estimate of the volume sampled by a Granton trawl. Recently, however, it appears that a number of Spanish vessels are using a high headline Polish trawl. Their catches

are also predominantly of hake and so the higher estimate of 3.36 M tons in the 0–4-fath scan can be justified.

On page 15 of Cushing (1968) the acoustic densities on the Cape Town grounds and on the Lüderitz grounds are compared with the actual catches. Off Cape Town in 220 fath, the acoustic density corrected to 225 fath should be 0.288 tons/hr (not 1 ton/hr) as compared with an observed catch of 0.5 tons/hr. Off Lüderitz in 220 fath, an acoustic density correction to 225 fath should be 0.864–2.88 tons/hr (not 3–10 tons/hr) as compared with an observed catch of 1.5–2.5 tons/hr.

The Estimation of Numbers of Fish

The usual way of estimating numbers of fish is to class them into age-groups or length-groups, which has the advantage that growth rates and mortality rates can be calculated. Ideally, if signals from single fish were recorded in signal strength, estimates of numbers and size could be obtained from the observations of signals. A very rough approximation to this procedure was used off South Africa, making use of the slope of the continental shelf and of the data given in Fig. 4, showing that bigger fish live in deeper water. A chart was drawn of numbers/$10^6 m^3$ as at a mean length of 46 cm and expressed at $n/10^4 m^2$ of surface on the chart. A bathymetric chart was overlaid and the numbers within an interval of depth were summed. From the line of mean signal on depth in Fig. 4, depth intervals were transformed into specified intervals of length. So, following the numbers in depth contours, a length distribution of the total stock was obtained (Fig. 7) for the fathom above the sea bed.

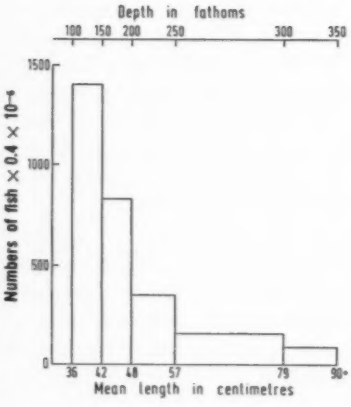

FIG. 7. Length distribution of single fish in the fathom off the bottom in February 1966 off South Africa from the cruise of HMS *Hecla*.

There is a bias in this length distribution because a sampling volume has been used appropriate to a fish of 46 cm long. The fish smaller than 46 cm are assumed to be counted in the sampling volume appropriate to a 46-cm

fish. Thus their density is underestimated. For the same reason the density of the larger fish is overestimated. So the numbers of small fish are underestimated and those of large fish are overestimated. The bias is absent in the total number, but a total weight derived from these numbers may perhaps be biassed.

The intervals of length increase with length because of the nature of the curve of mean signal on range in Fig. 4. If signals from all single fish were recorded in signal strength, then a length distribution of the stock could be estimated in equal length intervals. Further, with a simple age–length key the original observations in length could be converted to an age distribution in stock.

DISCUSSION

Certain preliminary requirements must be satisfied before any acoustic estimation of fish stocks can be attempted. First, the fish should be identified by effective capture and the stock estimate should be restricted to the depth zone of effective capture. Secondly, the fish should be recorded as individuals (and it is now clear that an estimate of signal strength is needed as each individual is recorded). Thirdly, the transducer should be calibrated and the amplifier should be monitored. Furthermore, the output of the transducer should be expressed in energy or in sound pressure and the signal at the amplifier should be expressed in the same units. These preliminary requirements can be readily achieved, often with commercial echo sounders.

Three separate advances have made it possible to estimate fish stocks acoustically. First is the estimation of target strength. A number of measurements have been made in the last decade for a variety of purposes. To estimate numbers of fish in a stock the measurements of target strength must be referred to a standard level of energy or of sound pressure. Secondly, the proper averaging of signals from individual fishes for periods of time leads to a statistical treatment within a defined volume. Thirdly, given the target strength of the fish, the volume appropriate to the size of fish can be specified. So the limit to the system is the range, or depth, at which the smallest fish can be detected. Larger fish can be detected at greater ranges in proportion to the ratio of the target strengths of the larger and smaller fish.

The technique of acoustic enumeration is of prime use to fisheries biologists. There are two main applications, the first of which is the estimation of stock and stock density independent of catch per unit effort. Not only can the problems of availability be attacked directly, but problems of population analysis may be sometimes simplified. The second application is that exploration can be made in such a way that an estimate of stock can be made by age-groups before fishing starts.

The same technique can be used by marine biologists interested in the sizes and numbers of animals. There is no reason why squids or euphausiids should not be enumerated by present methods using commercial echo sounders or their analogues aboard research vessels. A modification of the technique

might be used at high frequencies (in megacycles) to estimate numbers of zooplankton. But of course most of these animals can already be estimated adequately with high-speed tow nets.

The method described is relatively primitive in instrumentation. It is hoped that Midttun's method (1966) of automatically recording signal strength from single fishes can be used for data processing. A paper record would be a useful presentation for checking and measurement at sea. The bulk of the data could go directly on to magnetic tape, to be processed by a simple computer programme.

ACKNOWLEDGMENTS

I am grateful to the Hydrographer of the Royal Navy, Rear Admiral G. S. Ritchie, D.S.C., R.N., for work aboard HMS *Hecla* off South Africa and South West Africa. I am also grateful to Captain G. P. D. Hall, D.S.C., R.N., and the officers and men of HMS *Hecla* who allowed me to make the greatest use of their excellent oceanographic facilities.

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(APPENDIX *follows*)

APPENDIX

The Calculation of the True Volume Sampled by the Echo Sounder

(Prepared by J. G. K. Harris)[1]

Volume Sampled by Square Transducer

Consider a spherical shell having its centre on the surface of the sea, having internal radius r_2 and external radius r_1. A square transducer samples a saucer-shaped volume consisting of the portion of the shell lying within an angle θ of the downward vertical.

This volume is equal to $2\pi\left[r_1^3 - r_2^3\right](1 - \cos\theta)/3$.

Volume Sampled by Rectangular Transducer

In the case of a rectangular transducer, θ varies from a minimum of θ_β along the ship's course to a maximum of θ_α at right angles to it, and the portion of the spherical shell described is approximately elliptical in shape. Appendix Fig. 1 shows the shape of a quarter of such a shell in the case when $r_2 = 49$ fath, $r_1 = 50$ fath, $\theta_\alpha = 14°$, and $\theta_\beta = 9°$.

If θ_α and θ_β are assumed to be sufficiently small, the area of an ellipse on the surface of a sphere of radius r approximates to $\pi(r\theta_\alpha)(r\theta_\beta) = \pi r^2\theta_\alpha\theta_\beta$, and the area of a circle on the surface of the same sphere approximates to $\pi(r\theta)^2 = \pi r^2\theta^2$.

In practice $\theta \not> 14°$ and the error in these approximation is less than 0.5%. The area of the ellipse is therefore approximately equal to the area of the circle described by $\theta = \sqrt{\theta_\alpha\theta_\beta}$, and the volume sampled by the rectangular transducer is approximately equal to

$$2\pi\left[r_1^3 - r_2^3\right]\left(1 - \cos\sqrt{\theta_\alpha\theta_\beta}\right)/3.$$

True Volume Sampled

In practice the ship is steaming forward and the echo sounder samples a number of overlapping volumes. Although this results in several signals being received from one fish, these are recognizable as coming from a single object and the true volume sampled is therefore an almost continuous band along the ship's course.

The cross section of the volume sampled is the projection of a single elliptical shell on to a vertical plane at right angles to the ship's course. The shape of this area is shown drawn to scale in App. Fig. 1A, and diagrammatically in App. Fig. 2.

$$R = r_2\,\frac{(\sin^2\theta_\alpha + (\cos\theta_\beta - \cos\theta_\alpha)^2)}{2\,(\cos\theta_\beta - \cos\theta_\alpha)},$$

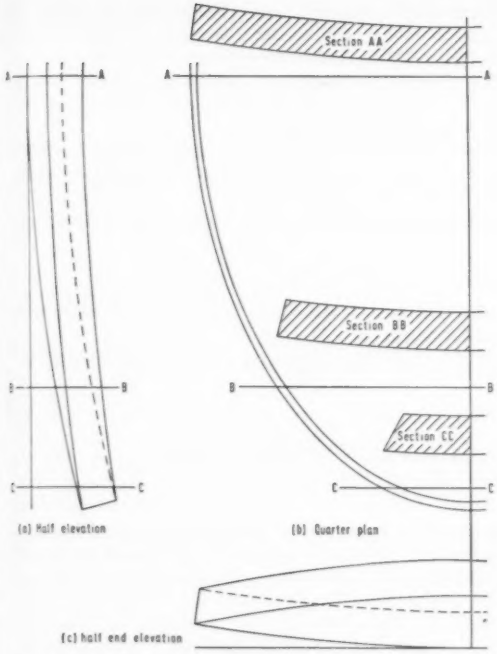
and if φ is the angle subtended by BC at X.

$$\varphi = \sin^{-1}\left[\frac{r_2\sin\theta_\alpha}{R}\right]$$

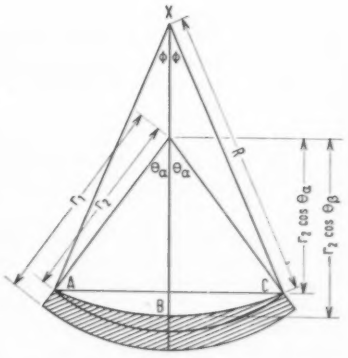
$$= 2\tan^{-1}\left[\frac{\cos\theta_\beta - \cos\theta_\alpha}{\sin\theta_\alpha}\right].$$

The area of the cross section can be calculated by assuming the arc ABC in App. Fig. 2 to approximate to a circle of radius R, centre X. R can then be calculated, and is given by

[1]Fisheries Laboratory, Ministry of Agriculture, Fisheries and Food, Lowestoft, England.



APP. FIG. 1. Scale drawing of quarter elliptical shell for $r_1 = 50$ fath, $r_2 = 49$ fath, $\theta\alpha = 14°$, and $\theta\beta = 9°$.



APP. FIG. 2. Diagrammatic projection of elliptical shell onto vertical plane at right angles to ship's course.

Let the area of the cross section = Z. Then

$$Z = r_1^2\,\theta_\alpha - \frac{r_2^2 \sin 2\,\theta_\alpha}{2} - \frac{R^2}{2}\,(2\,\varphi - \sin 2\,\varphi).$$

If D is the distance steamed by the ship, V_T is the true volume sampled by the echo sounder, given by

$$V_T = DZ$$

$$= D\left[r_1^2\,\theta_\alpha - \frac{r_2^2 \sin 2\,\theta_\alpha}{2} - \frac{R^2}{2}\,(2\,\varphi - \sin 2\,\varphi)\right].$$

ERROR DUE TO DISCONTINUITY

Owing to the curved shape of the individual volume sampled and the finite spacing between samples, the assumption of continuity is not strictly valid, and it is necessary to investigate the magnitude of the error which can arise.

Appendix Fig. 3 shows a cross section along the ship's course, showing the manner in which successive samples overlap. The shaded areas represent portions of the assumed continuous sample which never came into the range of the echo sounder, and the ratio of the shaded area to the area of the whole band represents the error resulting from the assumption of continuity.

It is not possible to derive a simple formula for this error, but it has been investigated for a particular case. The sample investigated is of an echo sounder sampling a shell 1 fath thick (2 m) at depths of 50–300 fath (100–600 m), the samples being taken at one every 2 fath (4 m) along the course of the ship. At 50 fath the error varies from 6.6% on the centre line to 5.0% near the edge. It then increases rapidly over the outside 1% of the shell to 100% at the extreme edge. The overall error at 50 fath is approximately 6%.

As the depth increases, the volume sampled is increased, but the error volume is almost constant. As a result the accuracy is improved with depth, and at 300 fath the error is reduced to approximately 2%.

In practice the errors will only exceed these figures if the frequency of sampling is decreased, or the angle of scan is increased.

Comparison with Number of Exclusive Volumes

In Cushing (1968) the ratio of V_T, the true volume sampled to V, the volume estimated by summing exclusive volumes, was wrongly estimated as 1.21.

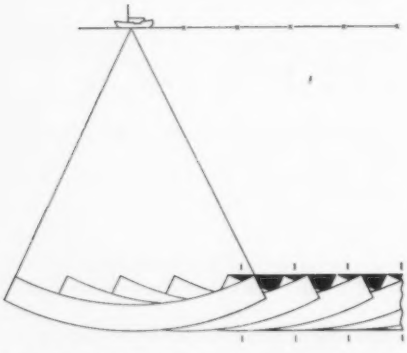
V is obtained by multiplying the volume of a single sample by $D/2r_1 \sin \theta_\beta$, the number of exclusive volumes in a distance, D.

$$V = \frac{\pi D\left[r_1^3 - r_2^3\right]\left(1 - \cos\sqrt{\theta_\alpha\theta_\beta}\right)}{3r_1 \sin\theta_\beta}$$

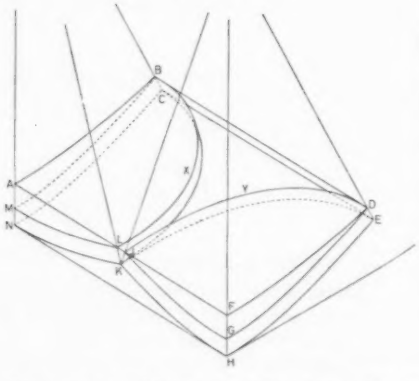
Appendix Fig. 4 shows diagrammatically how the summing of exclusive volumes leads to an under estimate of the true volume sampled. Two quarter exclusive volumes LKMNBCX and JKGHDEY are shown. The volume sampled is more truly represented by the volume ANBCDEFH.

$$\text{The ratio } \frac{V_T}{V} = \frac{3r_1 \sin\theta_\beta\left[2r_1^2\,\theta_\alpha - r_2^2 \sin 2\,\theta_\alpha - R^2\,(2\,\varphi - \sin 2\,\varphi)\right]}{2\pi\left[r_1^3 - r_2^3\right]\left(1 - \cos\sqrt{\theta_\alpha\theta_\beta}\right)}$$

In the case where $\theta_\alpha = 14°$ and $\theta_\beta = 9°$ and $r_1 - r_2 = 1$ fath, V_T/V is found to vary from 1.79 for $r_1 = 50$ fath to 4.36 for $r_1 = 300$ fath though in each case a small correction, $\leq 6\%$, should be made for discontinuty (see above).



App. Fig. 3. Vertical cross section through ship's course to show degree of overlap between successive elliptical shells.



App. Fig. 4. Diagram to show error due to summing exclusive volumes (see text).

Two New Species of *Gyrocotyle* (Monogenea) from *Hydrolagus affinis* (Brito Capello) (Holocephali)[1]

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ABSTRACT

Two new species of *Gyrocotyle* have been found in the intestine of the deepwater chimaera *Hydrolagus affinis* of the northwest Atlantic. *Gyrocotyle* had not previously been recorded from this host species.

Descriptions are provided for ♀-mature and ♂-mature specimens of *Gyrocotyle major* n.sp. and ♀-mature specimens of *Gyrocotyle abyssicola* n.sp. The systematic status, distribution, and some host relationships of these species are discussed. Within the subgenus *Amphiptyches*, two groups of species are recognized: the *urna*-group, including *G. major*, and the *confusa*-group including *G. abyssicola*. Geographical variation is shown by *G. major*. Allometric growth of different parts of the body in *G. major* is described. These *Gyrocotyle* specimens are the largest yet recorded, *G. major* attaining a maximum length in our collection of 200 mm and *G. abyssicola* of 138 mm. The size of *G. major* increases with size of host.

INTRODUCTION

The chimaeroid fishes are hosts to the genus *Gyrocotyle*. Until recently the Gyrocotylida were usually placed in the class Cestoda and the subclass Cestodaria. However, Llewellyn (1965) has developed an argument relating them rather to the class Monogenea, in which the Gyrocotylida may be considered as a subclass.

In the 20th century, notable contributions to the study of the genus *Gyrocotyle* have been made by Watson (1911), Dollfus (1923), Fuhrmann (1930), Lynch (1945), Mendívil-Herrera (1946), Joyeux and Baer (1951), and Manter (1951).

The present paper includes what are apparently the first records of *Gyrocotyle* from the deepwater chimaera *Hydrolagus affinis* (Brito Capello, 1868); the description of the two species of *Gyrocotyle* found; an account of the distribution and of some parasite–host relationships for these *Gyrocotyle*.

This is the first time that species of *Gyrocotyle* have been reported from the Canadian east coast. Until now the only Canadian records were of two

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species of *Gyrocotyle* occurring in *Hydrolagus colliei* (Lay and Bennett) in British Columbian waters (Wardle, 1932). The two Pacific Coast species are evident from Wardle's photograph, although Wardle recognized only one species, which he erroneously called *Gyrocotyle urna*.

MATERIALS AND METHODS

On August 14–23, 1967 the *A. T. Cameron* (Mr E. M. LeGrow technician-in-charge acting under plans prepared by the junior author) fished the northwest Atlantic by longline in depths of 1750–2450 m. From 31 deepwater chimaeras, *Hydrolagus affinis*, taken on this cruise, 45 specimens of *Gyrocotyle* were obtained (Fig. 1, Table I).

The *H. affinis* were frozen on board the research vessel. About 5 weeks later at the St. John's Biological Station the fish were thawed in ice and examined by the junior author. The process of examination took a number of days and there was some but not much spoilage indicated by slight darkening in a few of the specimens of *Gyrocotyle* found. Usually, but not in all cases, the parasites were relaxed when measured fresh by the junior author but there was usually some, but not great, contraction on preservation. The first few *Gyrocotyle* collected were preserved directly in 5% formalin. The remainder were relaxed in crushed ice, usually for several hours, preserved for a few hours or overnight in 2% formalin, and then transferred to 50% isopropyl alcohol. The parasites were sent to the senior author for systematic examination.

It was determined that two new species of gyrocotylids were present in the collection, *Gyrocotyle major* (Fig. 2–5) and *Gyrocotyle abyssicola* (Fig. 5).

For the fish lengths used in the host–parasite comparisons the greatest total length of *H. affinis* is not used because the tip of the caudal filament was sometimes broken off. The length, as taken on a measuring board, from the snout to the upper origin of the caudal fin is used and is directly comparable for all the *H. affinis* specimens.

The ♀-mature specimens of the parasite are of such a large size, that whole mounts cannot successfully be prepared. Several specimens were cleared in methyl benzoate. This procedure is a necessity for the proper study of the spines (at least when these are colourless) and of the internal organs. Some specimens were cross-sectioned with a razor; a microtome cannot be applied efficiently for the study of the gross morphology of such large animals. The ♂-mature specimens were all prepared as balsam whole mounts. Stains were not used because they generally obscure certain details.

Part of the material is kept in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RMNH); the rest is in the collection of the Biological Station of the Fisheries Research Board of Canada, St. John's, Nfld. (coll. St. John's).

The fresh length and greatest width were taken mainly in the relaxed condition before preservation, but all measurements of the parasites and all dimensions expressed in percentages of length or width refer to preserved specimens unless measurement in the fresh condition is especially mentioned.

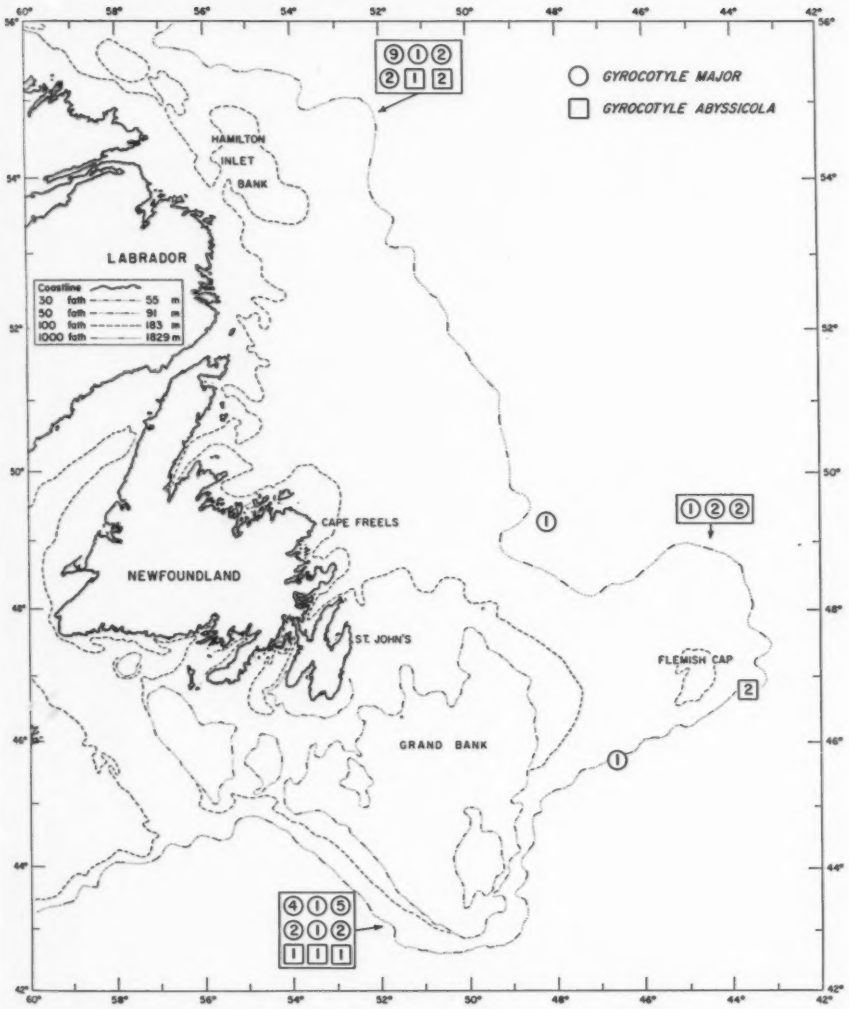

FIG. 1. Distribution and abundance of *Gyrocotyle major* and *G. abyssicola* in *Hydrolagus affinis* of the northwest Atlantic, caught by the *A. T. Cameron*, August 14–23, 1967.

The photographs of *Gyrocotyle* in the fresh condition were taken after the parasites were relaxed in crushed ice for 1 to several hours after removal from the fish; and those in the preserved condition after the above treatment, plus preservation in 2% formalin overnight and then in 50% isopropyl alcohol.

TABLE I. Distribution and occurrence of *Gyrocotyle major* and *G. abyssicola* in relation to its host, *Hydrolagus affinis*.

Locality	Position at midline N lat	Position at midline W long	Depth (*m*)	Temp (*C*) (Depth of temp, *m*)	No. *H. affinis* examined for *Gyrocotyle*	No. *Hydrolagus* infested with: *G. major*	*G. abyssicola*	*G. major* or *G. abyssicola*[a]	No. *Gyrocotyle*: *G. major* ♀ mature	*G. major* ♂ mature	*G. abyssicola* ♀ mature	*Hydrolagus* length (*mm*)[b] Range	Avg	Date of capture, 1967
Hamilton Inlet Bank	54°52′15″	51°59′30″	2300	3.34 (1700)	8	4	2	6	13	1	3	797–1179	979	Aug. 14
Off Cape Freels, Nfld. and N of E Grand Bank	49°15′30″	48°16′00″	2200–2250	3.16 (1660)	3	1	0	1	1	0	0	835–1195	1045	" 17
N of Flemish Cap	49°03′30″	44°32′00″	2200–2350	3.32 (1680)	4	3	0	3	5	–	0	888–1202	1056	" 18
S of Flemish Cap	46°48′00″	43°41′45″	2000–2450	3.42 (1680)	1	1	0	1	0	0	2	1091	1091	" 19
Off E Grand Bank	45°40′48″	46°40′15″	2250–2300	3.53 (1680)	1	1	0	1	0	1	0	777	777	" 20
Off SW Grand Bank	43°03′30″	52°02′45″	1750–2200	3.68 (1700)	13	6	3	9	14	2	3	763	763	" 22
Off SW Grand Bank	44°31′30″	54°43′30″	2000–2100	3.68 (1620)	1	0	0	0	0	0	0	597–1017	783	" 23
Total			1750–2450	3.16–3.68 (1620–1700)	31	16	5	21	33	4	8	597–1202		

[a]No *Hydrolagus affinis* was infested with both *G. major* and G. *abyssicola*.
[b]Length snout to upper origin caudal fin. Includes all *H. affinis* examined for *Gyrocotyle*.

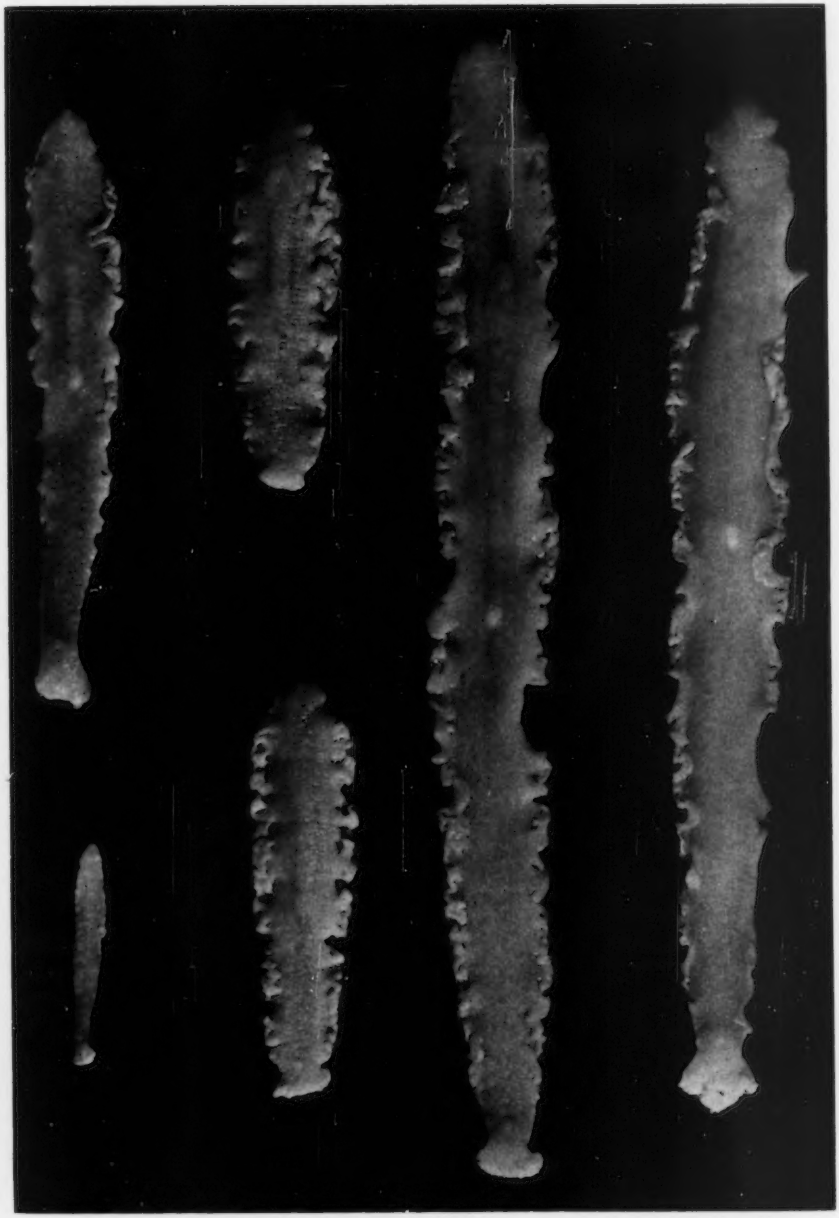

FIG. 2. *Gyrocotyle major* from *Hydrolagus affinis*, August 1967, ×ca. 0.9, in fresh condition, all in dorsal view except the smallest specimen. All are ♀-mature except the smallest specimen which is ♂-mature. Total fresh lengths (from lower to upper and from left to right) were: 35, 90, 68, 66, 185, and 162 mm.

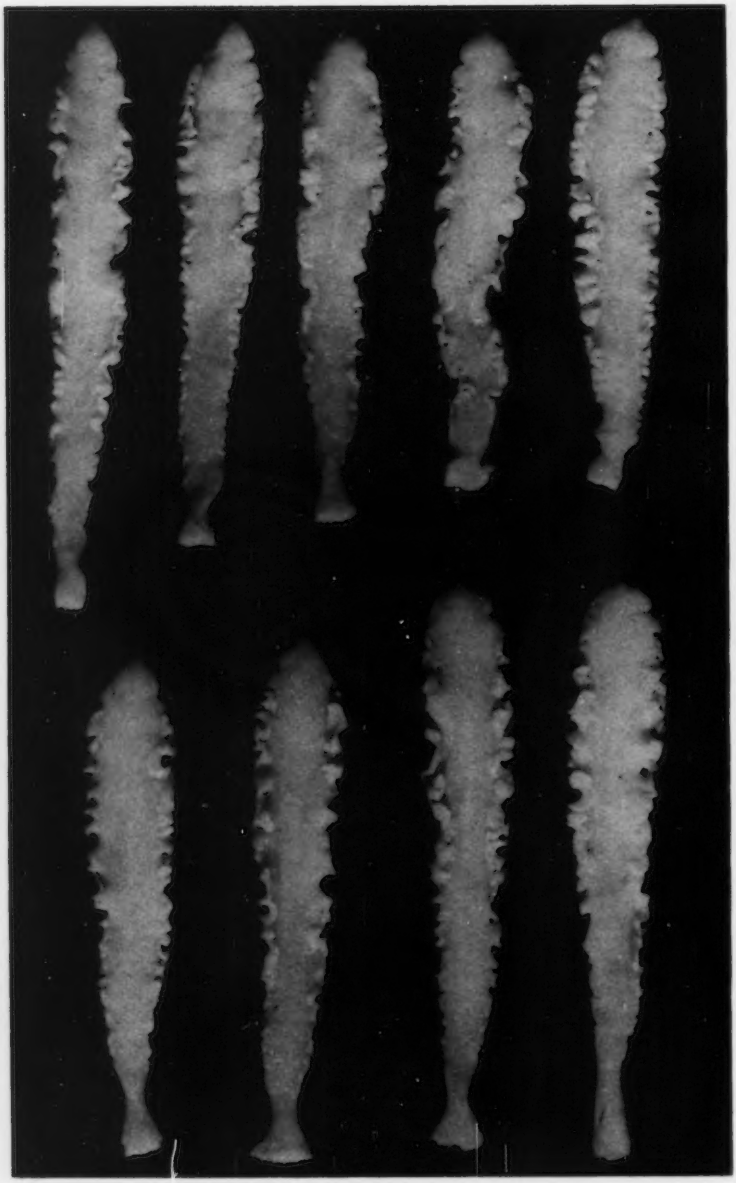

FIG. 3. *Gyrocotyle major* (paratypes), August 1967, approximately natural size, in fresh condition, all from a single immature female host *H. affinis*, 918 mm total length, snout to upper origin of caudal fin, taken off Hamilton Inlet Bank (host (autopsy) no. 23). Total fresh lengths of the nine parasites ranged from 66 to 85 mm. In order from left: *upper row* — three dorsal, ventral, and dorsal views; *lower row* — dorsal, ventral, and two dorsal views.

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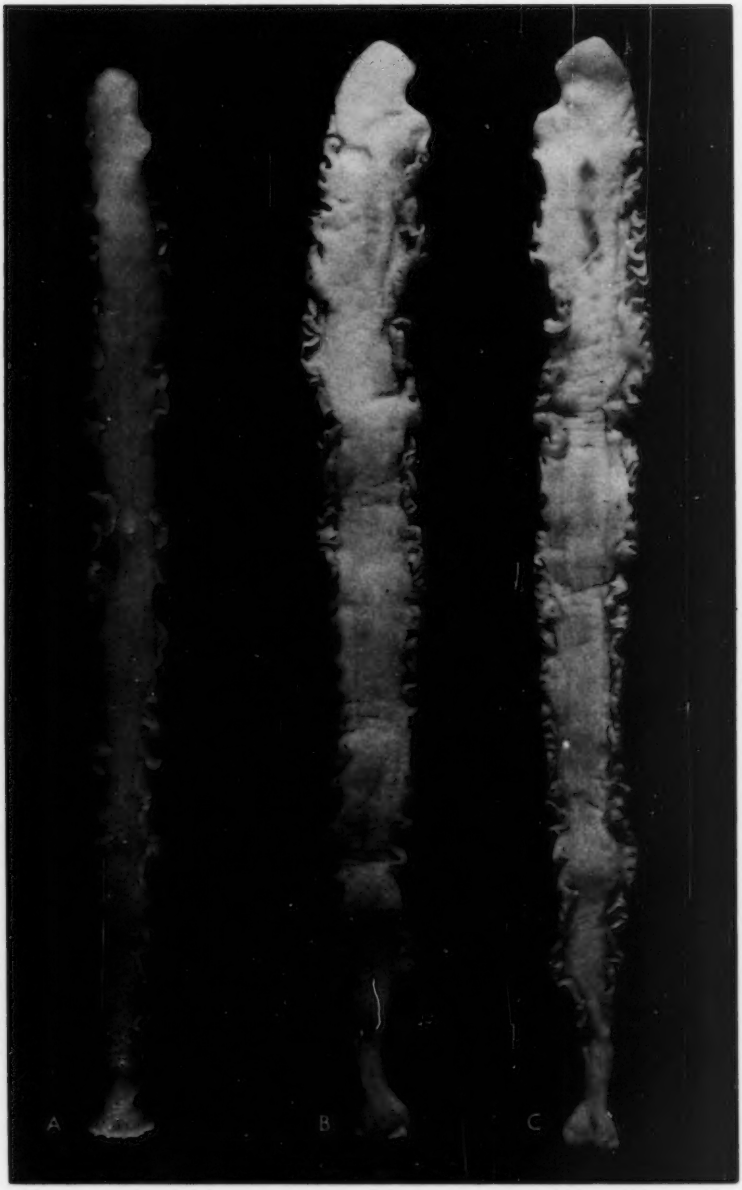


FIG. 4. *Gyrocotyle major*, August 1967, ×0.84: A, dorsal view, in fresh condition: B, dorsal and C, ventral view in preserved condition. A, 192 mm total fresh length from mature female host *H. affinis*, 1202 mm total length, snout to upper origin of caudal fin, taken north of Flemish Cap (host (autopsy) no. 18); and B, C, (paratype), 200 mm total fresh length from mature female host *H. affinis*, 1179 mm total length, snout to upper origin of caudal fin, taken off Hamilton Inlet Bank (host (autopsy) no. 29).

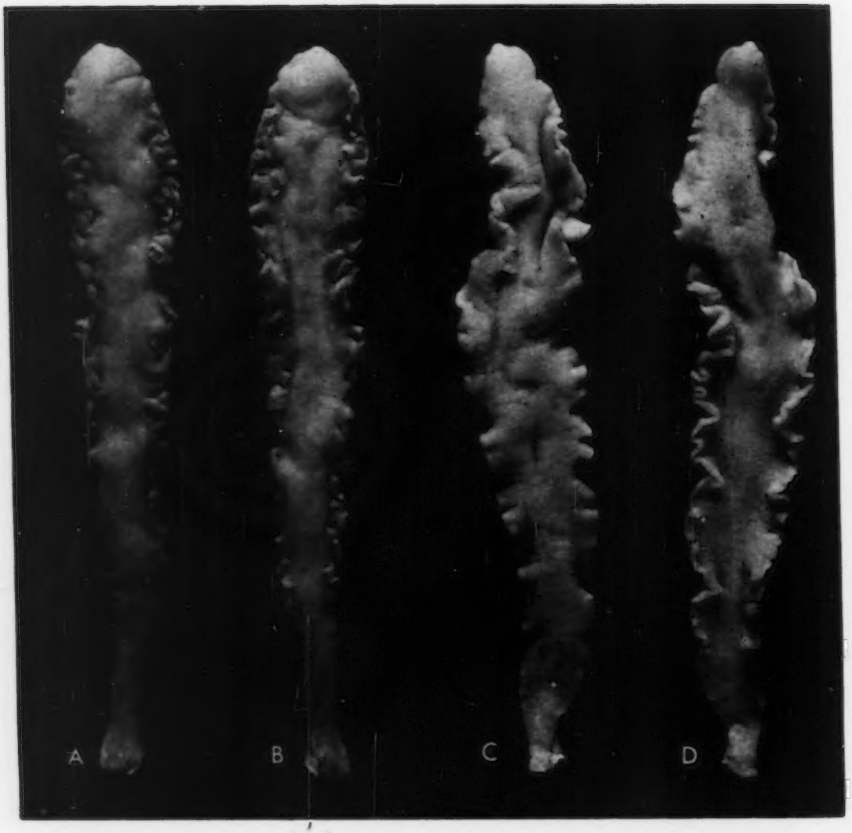


FIG. 5. A, dorsal and B, ventral views of a preserved *G. major* (paratype), 83 mm fresh length, ×1.33. See the same specimen in fresh condition, dorsal view, natural size on the lower right of Fig. 3; C, dorsal and D, ventral views of a preserved *G. abyssicola* (holotype), 111 mm fresh length, natural size, from immature female host *H. affinis*, 908 mm total length, snout to upper origin of caudal fin, taken off Hamilton Inlet Bank (host (autopsy) no. 26).

RESULTS

Gyrocotyle major n.sp.

DESCRIPTION

Type locality: Atlantic Ocean, off Hamilton Inlet Bank (Labrador), 54°52′15″N, 51°59′30″W, depth 2300 m. Type host: *Hydrolagus affinis* (Brito Capello) (Holocephali). Location: intestine.

Material: Holotype: ♀-mature specimen, autopsy no. 29, RMNH coll. no. 6358; Allotype: ♂-mature specimen, autopsy no. 25, RMNH whole mount no. 6359. Paratypes: 3 specimens, autopsy no. 23, RMNH coll. no. 6360; 9 specimens, autopsy no. 22, 23, 25, and 29, coll. St. John's.

Atlantic Ocean, off Cape Freels (Newfoundland), and N of eastern Grand Bank 49°15′30″N, 48°16′00″W, depth 2200–2250 m, 1 specimen, autopsy no. 20, coll. St. John's.

Atlantic Ocean, off Newfoundland, N of Flemish Cap, 49°03′30″N, 44°32′00″W, 2200–2350 m, 1 specimen, autopsy no. 6, RMNH coll. no. 6361; 4 specimens, autopsy no. 6, 18, and 32, coll. St. John's.

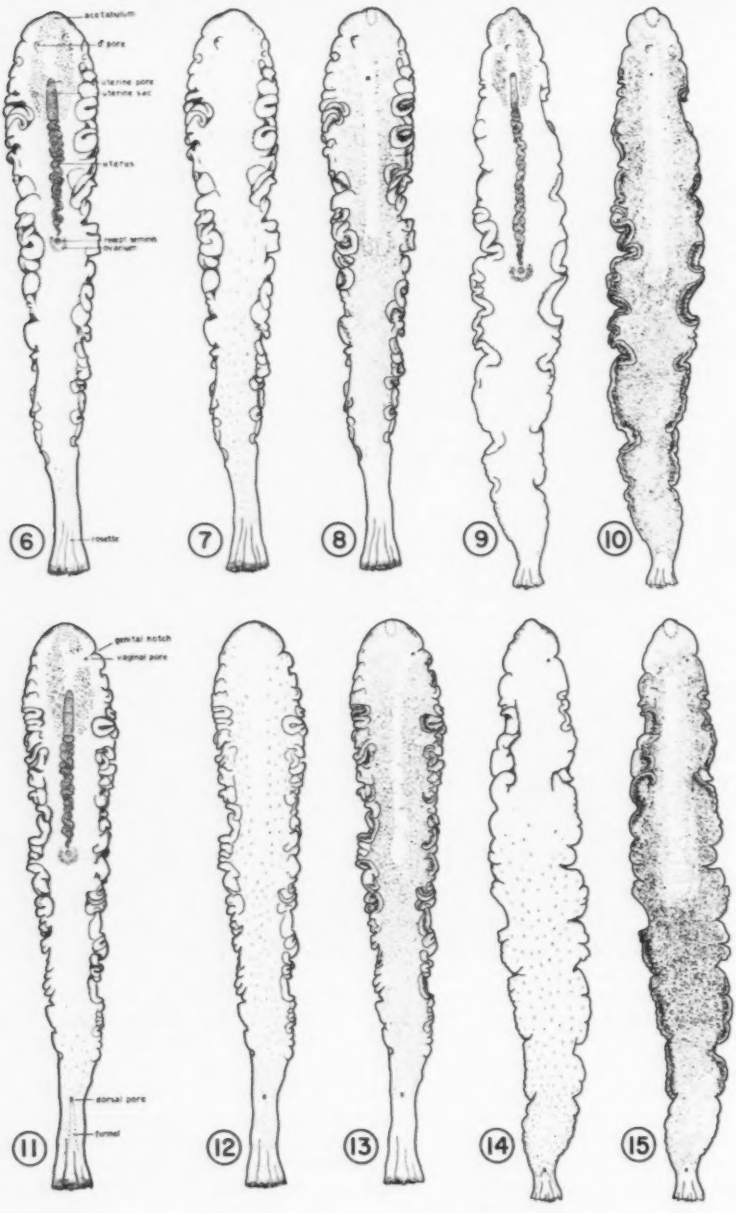
Atlantic Ocean, off eastern edge Grand Bank (Newfoundland), 45°40′48″N, 46°40′15″W, depth 2250–2300 m, 1 ♂-mature specimen, RMNH whole mount no. 6362.

Atlantic Ocean, off southwest edge Grand Bank (Newfoundland), 43°03′30″N, 52°02′45″W, depth 1750–2200 m, 2 ♂-mature specimens, autopsy no. 11, whole mounts, coll. St. John's; 4 specimens, autopsy no. 13, 16, and 30, RMNH coll. no. 6363; 9 specimens, autopsy no. 16, 30, 31, and 33, coll. St. John's.

DESCRIPTION OF ♀-MATURE SPECIMENS (HABITUS: FIG. 6 AND 11)

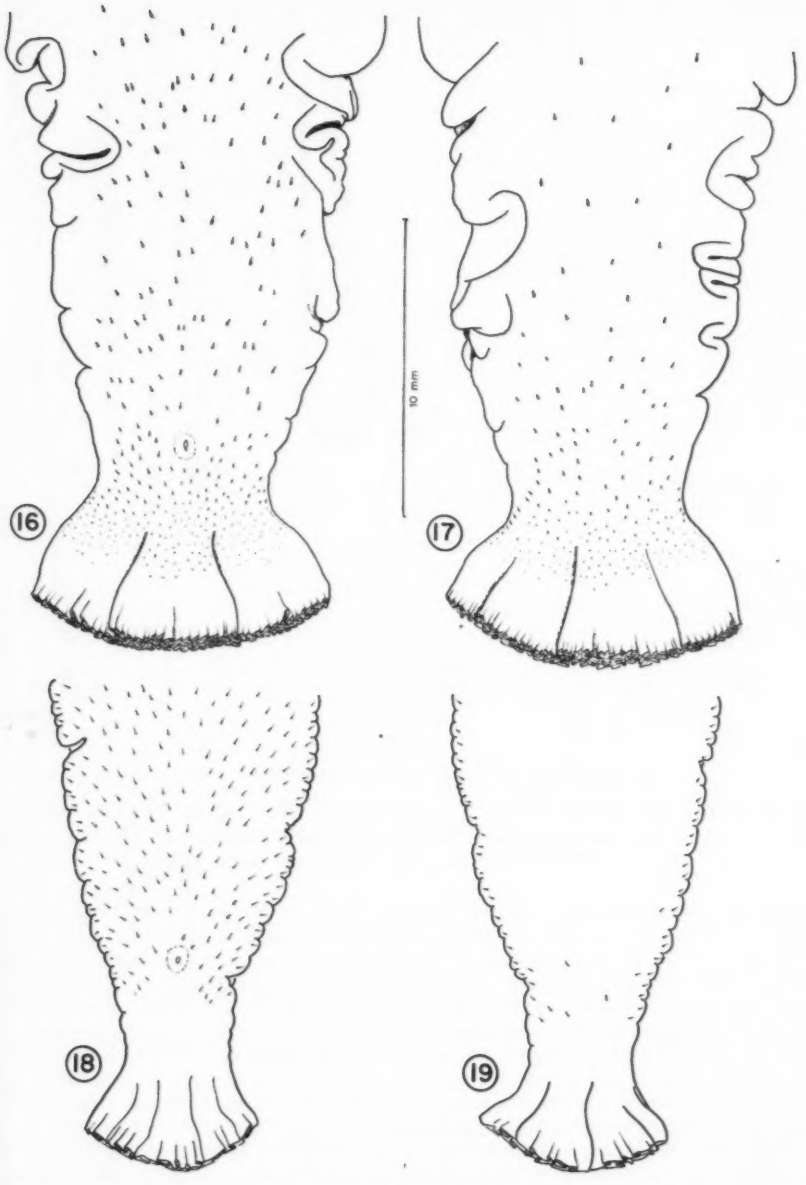
The fresh length of the body is 46–200 mm, the approximate greatest fresh width 9–23 mm. The level of the genital notch is 5–10% (average 7.5%) of the total length distant from the anterior end (Fig. 32). The length of the acetabulum is about 50% of the distance from the anterior end to the level of the genital notch. Lateral ruffles are present, numbering from about 15 to more than 35; they are of the complicated type, with a great dorsoventral amplitude and with a few too many secondary undulations. The width of the rosette depends much on the state of contraction, but it is only in an exceptional case somewhat smaller than 50% of the body width; it is of the complexly folded type. The spines are of the *urna*-type (Fig. 20, 22, 24, and 25). The number of acetabular spines varies from about 15 to about 70; they may form a compact group, but they may also extend backwards and shade off into the dorsal body spines (Fig. 27). In most specimens most acetabular spines have a length of 250–300 μ, the longest spine of the group reaching a length of 350–450 μ; in nearly all specimens they are longer than the posterodorsal body spines. Body spines are present on the dorsal and ventral surfaces, but not on the lateral margins. They are most numerous on the posterior part of the body (Fig. 16 and 17). Posteriorly they gradually pass into the rosette spines, anteriorly they are gradually becoming sparse. The dorsal body spines may be confined to the posterior third of the body (Fig. 11), but sometimes they extend forward, though widely separated, to the acetabular spines (Fig. 12). An intermediate situation can be observed in most specimens. Spines are only exceptionally present on the frills and dorsal to the uterus and the receptaculum seminis. The ventral body spines are always less numerous and less widely distributed than the dorsal spines in the same animal. Sometimes they are confined to the posterior part of the body (Fig. 6), but most often they extend forward to the level of the posterior part of the uterus, and in one case even to the level of the genital notch (Fig. 7). The body spines are largest in the region just anterior to the dorsal pore, gradually becoming smaller anteriorly and posteriorly. The ventral spines are smaller than the dorsal spines. The greatest length of the body spines is about 300 μ in most specimens; infrequently the greatest length is more than 300 μ, up to 400 μ. The rosette spines encircle the basal part of the rosette. Generally they are extremely numerous; hundreds of them may be present. They are remarkably small, most of them being only 40–60 μ long.

The male genital pore is situated at $\frac{1}{3}$–$\frac{1}{2}$ of the distance from the median line to the genital notch, often on a distinct papilla. The two fields of testis follicles extend from the middle of the acetabulum to the posterior end of the uterine sac. The vaginal pore is located at about $\frac{2}{3}$ of the



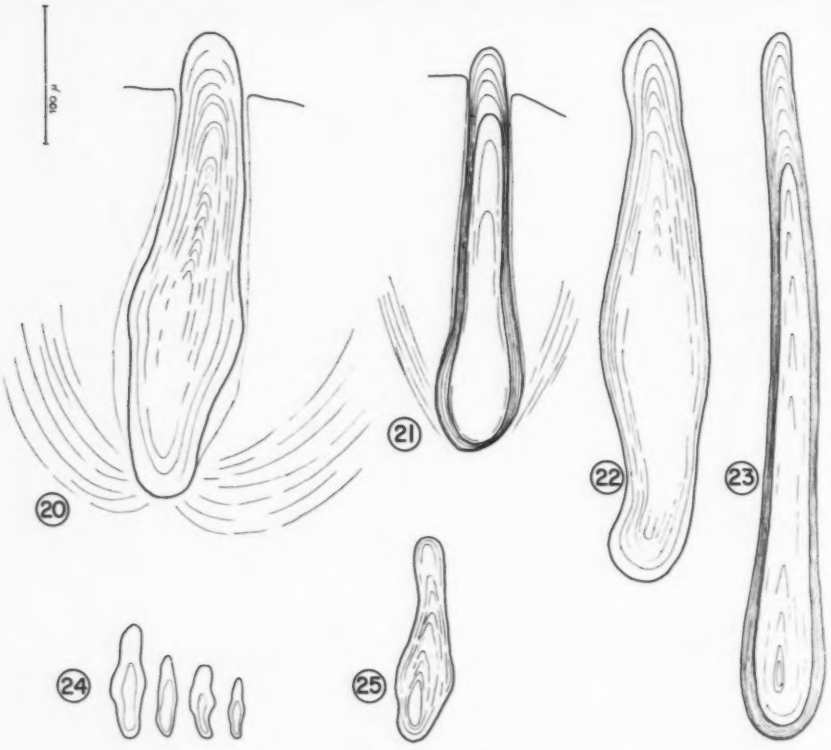
FIGURES 6–15. *Gyrocotyle major* and *G. abyssicola*, distribution of sex organs and spines (all semidiagrammatic).

Fig. 6: *G. major*, sex organs and spines (minimum), ventral; Fig. 7: *G. major*, spines (maximum), ventral; Fig. 8: *G. major*, vitellaria, ventral; Fig. 9: *G. abyssicola*, sex organs and spines, ventral; Fig. 10: *G. abyssicola*, vitellaria, ventral; Fig. 11: *G. major*, sex organs and spines (minimum), dorsal; Fig. 12: *G. major*, spines (maximum), dorsal; Fig. 13: *G. major*, vitellaria, dorsal; Fig. 14: *G. abyssicola*, spines, dorsal; Fig. 15: *G. abyssicola*, vitellaria, dorsal.



FIGURES 16–19. *Gyrocotyle major* and *G. abyssicola*, posterior part of body (all semidiagrammatic).

Fig. 16: *G. major*, dorsal; Fig. 17: *G. major*, ventral; Fig. 18: *G. abyssicola*, dorsal; Fig. 19: *G. abyssicola*, ventral.



FIGURES 20–25. *Gyrocotyle major* and *G. abyssicola*, spines.

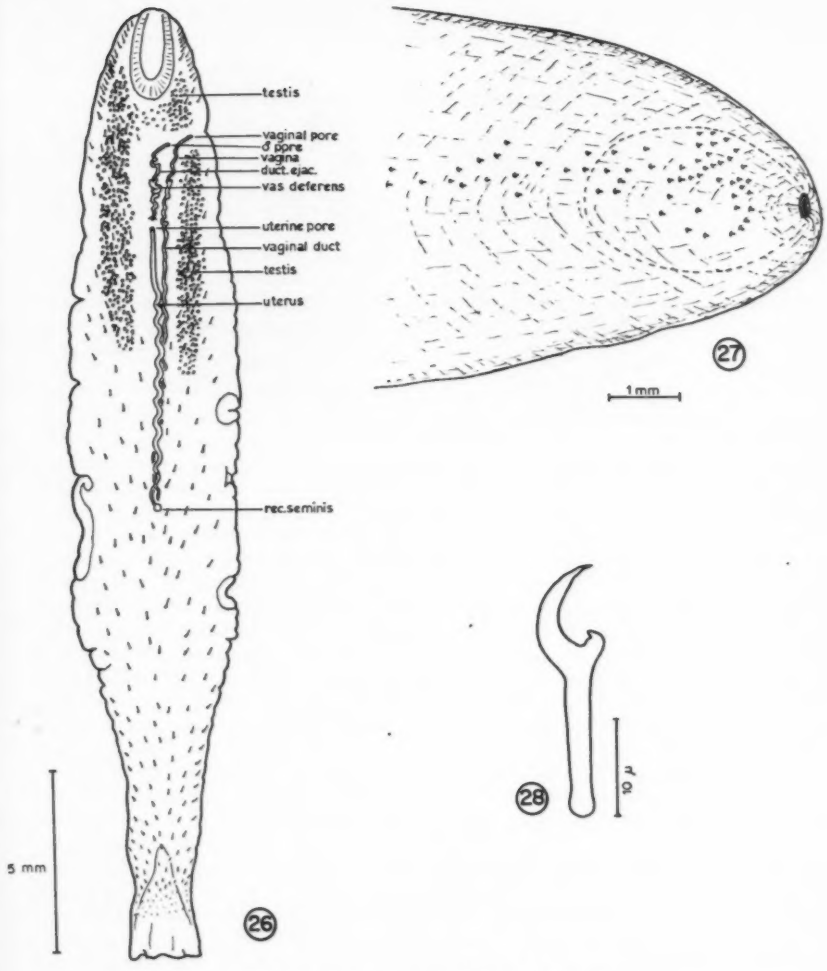
Fig. 20: *G. major*, body spine; Fig. 21: *G. abyssicola*, body spine; Fig. 22: *G. major*, acetabular spine; Fig. 23: *G. abyssicola*, acetabular spine; Fig. 24: *G. major*, rosette spines; Fig. 25: *G. major*, spine, intermediate between body spines and rosette spines.

distance from the median line to the genital notch. The receptaculum seminis is situated at a distance of 37–58% (average 46%) of the body length from the anterior end (Fig. 33). The length of the uterus is 17–30% (average 24%) of the body length; its width may reach 25% of the greatest width of the body. The length of the uterine sac is 5.5–12.5% (average 9%) of the body length. The uterine pore is located at a distance of 4–9 (average 7%) of the body length posterior to the level of the genital notch. The vitellaria extend from the level of the middle of the acetabulum to the level of the dorsal pore (Fig. 8 and 13); they are absent in a small region around the acetabulum, dorsal and ventral to the genital organs, and in a middorsal and midventral region anterior to the level of the dorsal pore. Sometimes they are present dorsal to the terminal genital ducts, anterior to the level of the uterine pore.

Eggs (Fig. 29) taken from the uterine pore have a length of 98–135 μ (average 116 μ) and a width of 59–89 μ (average 72 μ). The length/width ratio is 1.35–1.84 (average 1.61) (Fig. 31). The shell is about 2 μ thick. No larva is present.

DESCRIPTION OF ♂-MATURE SPECIMENS (HABITUS: FIG. 26)

The fresh length of the body is 21–35 mm, the approximate greatest fresh width up to 7 mm. The level of the genital notch is 11–17% (average 13%) of the total length distant from

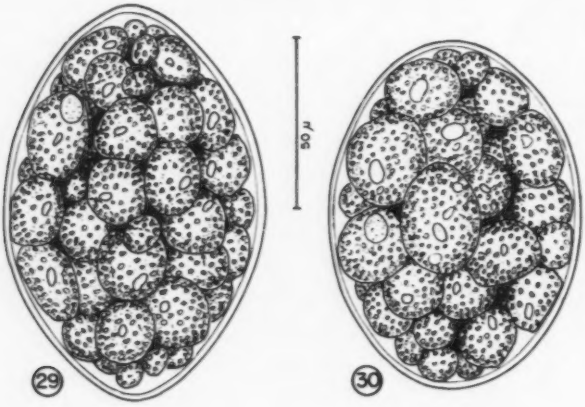


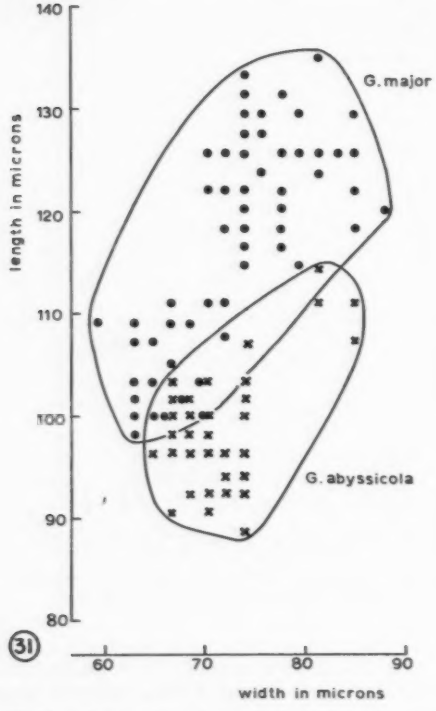
FIGURES 26–28. Some characteristics of *G. major*.

Fig. 26: *G. major*, ♂-mature specimen, dorsal; Fig. 27: *G. major*, head region, antero-lateral view; Fig. 28: *G. major*, larval hook.

the anterior end (Fig. 32). The length of the acetabulum is more than 50% of the distance from the anterior end to the level of the genital notch. Lateral ruffles are absent in three specimens, but in the largest specimen some are present. The rosette is simple, without folds. The 10 larval hooks (Fig. 28) can still be observed in the wall of the anterior part of the funnel; their length is about 26 μ. The spines have the same morphology and dimensions as in the ♀-mature specimens; they are distributed over the whole length of the body.

The two fields of testis follicles extend to the middle of the uterus. The follicles have completely developed and sperm are present in the vas deferens. The receptaculum seminis is





FIGURES 29–31. *Gyrocotyle major* and *G. abyssicola*, comparisons of eggs.

Fig. 29: *G. major*, egg; Fig. 30: *G. abyssicola*, egg; Fig. 31: *G. major* and *G. abyssicola*, eggs, length/width relationships.

situated at a distance of 47–58% (average 52%) of the body length from the anterior end. The uterus is still a narrow, straight or slightly undulated tube. The ovarium and the vitellaria have not yet developed.

Gyrocotyle abyssicola n.sp.

Type locality: Atlantic Ocean, off Hamilton Inlet Bank (Labrador), 54°52′15″N, 51°59′30″W, depth 2300 m. Type host: *Hydrolagus affinis* (Brito Capello) (Holocephali). Location: intestine.

Material: Holotype: ♀-mature specimen, autopsy no. 26, RMNH coll. no. 6364. Paratypes: 1 specimen, autopsy no 27 RMNH coll. no. 6365; 1 specimen, autopsy no. 27, coll. St. John's.

Atlantic Ocean, off Newfoundland, S of Flemish Cap, 46°48′00″N, 43°41′45″W, depth 2000–2450 m, 2 specimens, coll. St. John's.

Atlantic Ocean, off southwest edge Grand Bank (Newfoundland), 43°03′30″N, 52°02′45″W, depth 1750–2200 m, 1 specimen, autopsy no. 1, RMNH coll. no. 6366; 2 specimens, autopsy no. 10 and 12, coll. St. John's.

Description of ♀-Mature Specimens (Habitus: Fig. 9)

The fresh length of the body is 106–138 mm, the approximate greatest fresh width up to 19 mm. The level of the genital notch is 5.7–8.6% (average 7%) of the total length distant from the anterior end (Fig. 32). The length of the acetabulum is about 50% of the distance from the anterior tip to the level of the genital notch. Lateral ruffles are present, of which up to 12 can be recognized. They are of the simple type, in general with a small dorsoventral amplitude and without secondary undulations. Large parts of the lateral margins are only notched. The width of the rosette is 30–45% (average 40%) of the body width; it is of the simply folded type. The spines are of the *confusa*-type (Fig. 21 and 23). The number of acetabular spines is up to about 70; they may form a compact group, but sometimes they extend backwards to the level of the genital notch, although they never merge with the body spines. In one specimen the length of the acetabular spines is 200–300 μ, in another 300–600 μ. The other individuals are intermediate. In most specimens they are longer than the posterodorsal spines. Dorsal, ventral, and lateral body spines are present. They are most numerous anterior to the dorsal pore (Fig. 18 and 19). The dorsal body spines extend from the middle of the funnel region to the level of the uterus (Fig. 14), sometimes nearly reaching the uterine sac; they may be present on the ruffles. Ventral body spines are confined to the anterior half of the funnel region; they are extremely sparse, only two to five spines being present. Lateral body spines are confined to the posterior quarter of the body. The greatest length of the body spines is about 300 μ in most specimens, but in some specimens the spines may reach a length of 400–450 μ.

The male genital pore is situated only slightly to the right of the median line, sometimes on a distinct papilla. The two fields of testis follicles extend from the middle of the acetabulum to the posterior end of the uterine sac. The vaginal pore is located at about $\frac{2}{3}$ of the distance from the median line to the genital notch. The receptaculum seminis is situated at a distance of 42–50% (average 45%) of the body length from the anterior end (Fig. 33). The length of the uterus is about 20–30% of the body length; its width is 15–30% of the greatest width of the body. The length of the uterine sac is 3.5–7% of the body length. The uterine pore is located at a distance of 3–4.5% of the body length posterior to the level of the genital notch. The vitellaria extend from the level of the middle of the acetabulum to the anterior part of the funnel region (Fig. 10 and 15). They are absent in a small region around the vaginal pore, ventral to the genital organs, and in a small middorsal and midventral region around the dorsal pore.

Eggs (Fig. 30) taken from the uterine pore have a length of 89–114 μ (average 98 μ) and a width of 65–85 μ (average 71 μ). The length/width ratio is 1.20–1.55 (average 1.38) (Fig. 31). The shell is 1–1.5 μ thick. No larva is present.

Geographical Variation in *G. major*

Geographical variation has never been observed in gyrocotylids, which is not astonishing because no comparative study of different populations

has ever been undertaken. The present material suggests the presence of geographical variation in the distribution of the spines. There is an evident difference between the material from the northern-most and the southern-most localities that lie at a distance of about 1300 km apart.

Specimens from the locality off Labrador have the smallest number of spines. The dorsal spines are often confined to the posterior part of the body (Fig. 11) and only in some specimens do some spines reach the level of the posterior part of the uterus.

On the contrary, all specimens from the southern-most locality have many spines. The dorsal spines extend at least to the anterior half of the uterus. All specimens with spines distributed over the whole length of the body belong to the southern-most population.

Only very few specimens from other localities are available. In all of them the anterior border of the dorsal spines lies somewhere across the uterus.

A Sinistral Specimen of *G. major*

In all species of Gyrocotylida the genital notch, the male pore, and the vaginal pore are normally located on the right side of the body. However, these organs are situated on the left side of the body in one of the specimens of autopsy no. 30. As far as we are aware such an abnormality has never been reported in the literature, and we have not observed it previously, although we have studied several hundred specimens, including nearly all known species.

Distribution

within the host

The *Gyrocotyle* were found mainly from the spiral valve region of the intestine of the *Hydrolagus*, often two adults so close together that they were taken out as one specimen. After the freezing and thawing, the contents of the intestines were fluid and a few of the parasites were in the gut anterior to the spiral valve section. Presumably this occurred after capture. The host *Hydrolagus* came from very deep water and the posterior part of the intestine was often turned inside out and extruded to the outside. Some *Gyrocotyle* could therefore have been lost while the fish was being pulled to the surface. One *Gyrocotyle* was found on the surface of the body of one of the *Hydrolagus*.

Sixty-eight percent of the 31 *Hydrolagus affinis* examined were infested with *Gyrocotyle*. Over three times as many were infested with *Gyrocotyle major* as with *Gyrocotyle abyssicola*. *Gyrocotyle major* was also the most numerous, 37 against 8 *G. abyssicola*. In 4 small *G. major*, 21–35 mm in fresh length, only the male sex organs were mature (♂-mature, sperm present in vas deferens, but no eggs in uterus) whereas in the remainder, 46–200 mm in fresh length, the female organs were also sexually mature (♀-mature, eggs in uterus). All *G. abyssicola* were ♀-mature (Table I).

The numbers of *Gyrocotyle* found in any one host, *H. affinis*, ranged from 0 to 9 with 1 and 2 most common and 4, 5, and 9 each occurring on one occasion, the larger numbers being all *G. major* (Table II). The two species were always in separate *H. affinis* hosts.

TABLE II. Number of *Gyrocotyle major* and *G. abyssicola* in relation to size, sex, and sexual maturity of *Hydrolagus affinis*.

Fish length snout–origin upper caudal fin (*mm*)	*G. major*		*G. abyssicola*	
	Female host	Male host	Female host	Male host
551–600	5	–	–	–
601–650	–	–	–	1
651–700	2	4	–	–
701–750	–	–	–	–
751–800	1, 0, 2, 0, 1	–	1,1	2
801–850	0, 0	1	–	–
851–900	1	–	–	–
901–950	2, 9	–	1	–
951–1000	0, 0	–	–	–
1001–1050	1, 2	0[a]	–	–
1051–1100	–	–	2	–
1101–1150	0,[a] 0,[a]	–	–	–
1151–1202	0,[a] 2,[a] 1,[a] 2[a]	–	–	–

[a]Host, *H. affinis*, sexually mature, otherwise host immature.

GEOGRAPHIC DISTRIBUTION

The distribution of both species of *Gyrocotyle* extended from the most northerly locality fished, east of Hamilton Inlet Bank, to the most southerly, south of the Grand Bank, over 700 nautical miles farther south (Fig. 1, Table I). They were abundant enough at both the northerly and southerly extremities that there is no reason to suppose that the parasites would not occur in the *H. affinis* both north and south of these localities.

The temperatures at the greatest depths that could be reached by the hydrographic wire, 50–770 m above the bottom, were little different (range 3.16–3.68 C) throughout the area. Judging by Smith et al. (1937) the temperature at the lowest level at which *H. affinis* was captured off Labrador should be about 3 C and it is therefore likely by reference to Table I that the *H. affinis* (and *Gyrocotyle*) were taken from bottom temperatures between about 3.0–3.7 C.

RELATIONSHIP BETWEEN LENGTH OF HOST AND LENGTH OF *Gyrocotyle*

The fresh length of the parasite compared with fish length (Table III) indicates strongly an increase in length of the *G. major* with increase in length of the female host fish. The same evidence is in favour of the retention of some individuals of this parasite by the host fish for many years and possibly for life. For the seven *G. major* and six *G. abyssicola* larger than 110 mm, there were never more than one or two parasites in the same fish. Thus there may also be some reduction in parasites as their size increases.

Dienske (MS, 1968) similarly found an increase in the weight of *Gyrocotyle urna* with increase in the weight of its host, *Chimaera monstrosa*.

The numbers of *G. major* in the male host and the numbers of *G. abyssicola* in both male and female hosts were much less than for *G. major* in female *H. affinis* hosts and did not show the parasite length – host length relationship. Male *H. affinis* do not grow to as great lengths as females of this species and there may not be as large *Gyrocotyle* present in the largest males as in the largest females. However, if the parasite length is more related to the host age than to its size, the parasite length – host length relationships in the male may be telescoped into a smaller range of host lengths.

TABLE III. Relationship of fresh length of *Gyrocotyle major* and *G. abyssicola* to length, sex, and sexual maturity of the host, *Hydrolagus affinis*.

Fish length snout–origin upper caudal fin (*mm*)	*G. major*		*G. abyssicola*	
	In female host (*mm*)	In male host (*mm*)	In female host (*mm*)	In male host (*mm*)
551–600	|46, 57, 62, 63, 66|[a]	–	–	–
601–650	–	–	–	|111|
651–700	|66, 68|	|83, 85, 98, 109|	–	–
751–800	|21, 29|35|88|	–	|106|132|	|106, 134|
801–850	–	|90|	–	–
851–900	|101|	–	–	–
901–950	|30, 99|66, 68, 68, 70, 73, 76, 80, 83, 85|	–	|111|	–
1001–1050	|72|134, 135|	–	–	–
1051–1100	–	–	|134, 138|	–
1151–1202	|121[b]|120,[b] 192[b]|185,[b] 200[b]|	–	–	–

[a]\| \| = parasites from the same host *H. affinis*.
[b]Host, *H. affinis*, sexually mature. Otherwise host immature.

These *Gyrocotyle* parasites from *H. affinis*, and especially *G. major* (Fig. 2–5), are by far the largest of all known gyrocotylids, reaching a fresh length of 185, 192, and 200 mm in the largest three specimens of *G. major* found (Table III). In addition to the *Gyrocotyle* recorded in Table III, another *G. major* of 162 mm (Fig. 2) was found on the surface of a *H. affinis*. The longest *G. abyssicola* found were 134 and 138 mm long (Table III).

The *Gyrocotyle* found in the same host *H. affinis* are usually, but not always, close enough in size that they could be considered likely to be the result of larval infection at the same time (Table III).

ALLOMETRIC GROWTH IN *G. major*

The summary of the fresh measurements of length and greatest width in *G. major* indicates that the relative width becomes less as the parasite

increases in length, from 19.6% of the total length at a parasite length of 42 mm to 10.7% at a parasite length of 192 mm (Table IV).

The anterior part of the body, i.e., the region anterior to the genital pores, shows negative allometric growth. The distance from the anterior end to the level of the genital notch becomes relatively smaller in larger animals (Fig. 32). In ♂-mature specimens it is about 13% of the body length on the average, and in the largest ♀-mature specimens about 5.5% on the average.

TABLE IV. Total length and greatest width of *Gyrocotyle major*. (Measurements were taken in fresh, usually fairly relaxed condition immediately after being taken from the fish.)

Parasite length range (*mm*)	Avg parasite length (*mm*)	Range parasite width (*% length*)	Avg parasite width (*% length*)	No. of *Gyrocotyle*
30–57	42	14.3–23.3	19.6	4
62–68	66	15.9–25.0	18.7	7
70–80	74	15.7–22.2	17.6	5
83–88	85	12.0–24.1	17.6	5
90–109	99	15.3–18.2	17.2	4
121–135	130	10.7–15.7	13.5	3
185–200	192	9.1–12.4	10.7	3

The same phenomenon was observed by Lynch (1945), who found that the ♂ pore is relatively much farther from the anterior end in small specimens and closer in those of maximum size.

This does not hold for the distance from the anterior end to the receptaculum seminis, which is here considered to be an important differential character. Throughout the life of the animals this distance does not deviate much from the average of 46% of the body length, as is shown in Fig. 33.

A most remarkable fact is that the few available data on these proportions for *G. abyssicola* fit so well in the material of *G. major*.

DISCUSSION AND CONCLUSIONS

SYSTEMATIC STATUS

The genus *Gyrocotyle* now includes 10 species, although some of them do not yet have a name. A list of the species is given here in order to facilitate a discussion of the systematic status of the new species. Such a list cannot simply be compiled from the literature. It is based on the unpublished results of a comparative study of material of most species, which was undertaken in order to arrive at a revision of the group. A systematic survey of the whole group will be published by J. van der Land and H. Dienske.

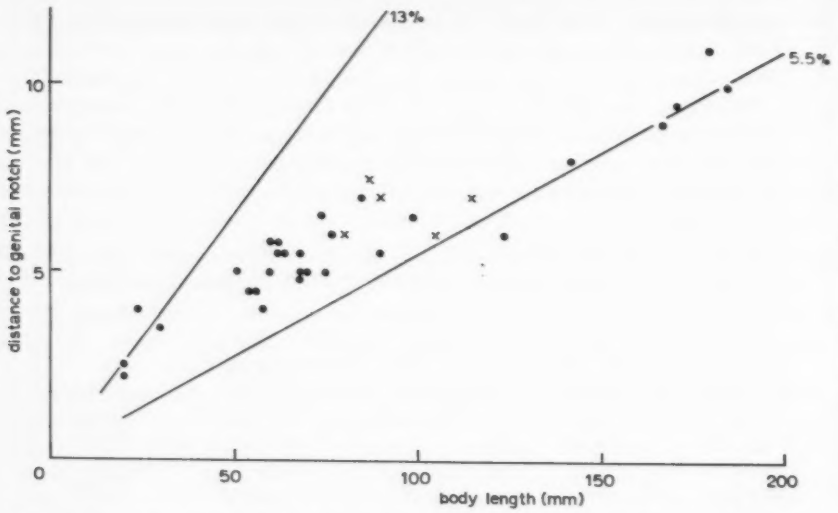


FIG. 32. *Gyrocotyle major* (●) and *G. abyssicola* (×), relation between distance from anterior tip to level of genital notch and body length. (Level of genital notch = the middle of the imaginary line directly across the body from the genital notch.)

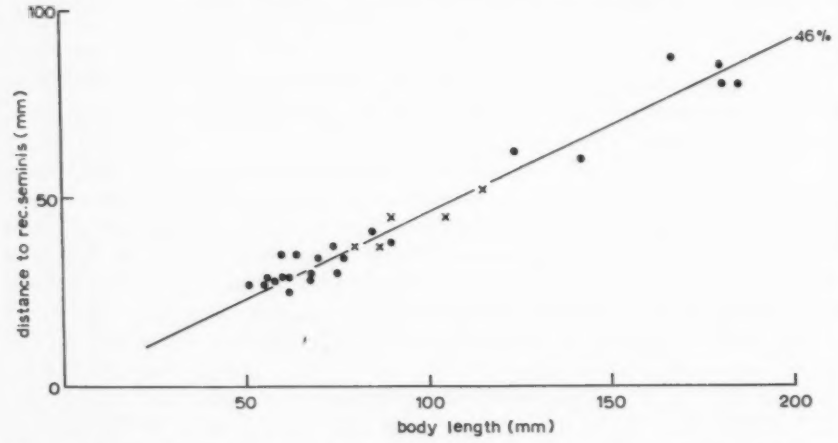


FIG. 33. *Gyrocotyle major* (●) and *G. abyssicola* (×), relation between distance from anterior tip to receptaculum seminis and body length.

SUBGENUS *Gyrocotyle* s.str.

1. *Gyrocotyle rugosa* Diesing, 1850; host: *Callorhinchus callorhynchus* (L.); distribution: southern oceans.

SUBGENUS *Amphiptyches* Wagener, 1852

2. *Gyrocotyle urna* (Wagener, 1852); host: *Chimaera monstrosa* L.; distribution: eastern North Atlantic, Mediterranean.

3. *Gyrocotyle major* n.sp.; host: *Hydrolagus affinis* (Brito Capello); distribution: western North Atlantic.

4. *Gyrocotyle fimbriata* Watson, 1911; host: *Hydrolagus colliei* (Lay and Bennett); distribution: eastern North Pacific.

5. *Gyrocotyle maxima* MacDonagh, 1927 (syn.: *G. meandrica* Mendívil-Herrera, 1946); host: *Callorhinchus callorhynchus* (L.); distribution: southern oceans.

6. *Gyrocotyle nigrosetosa* Haswell, 1902; host: *Hydrolagus ogilbyi* (Waite); distribution: western Pacific.

7. *Gyrocotyle* sp.; host: *Chimaera monstrosa* L.; distribution: eastern North Atlantic.

8. *Gyrocotyle abyssicola* n.sp.; host: *Hydrolagus affinis* (Brito Capello); distribution: western North Atlantic.

9. *Gyrocotyle* sp. (syn.: *G. urna* Lynch, 1945, non Wagener, 1852; host: *Hydrolagus colliei* (Lay and Bennett); distribution: eastern North Pacific.

10. *Gyrocotyle* sp.; host: *Callorhinchus callorhynchus* (L.); distribution: southern oceans.

Several species have not yet been described adequately. The best available descriptions are those of Lynch (1945), who described no. 4 and 9. Other useful descriptions are those of Mendívil-Herrera (1946) of no. 5, and of Manter (1951) of no. 1.

Both new species have undulated lateral margins, body spines, and a rather simple uterus. Consequently they belong to the subgenus *Amphiptyches* Wagener, 1852. Joyeux and Baer (1951) raised this group to the level of a genus, but Van der Land (1967) prefers to keep all species in one genus, mainly in the interests of the stability of nomenclature.

Within this subgenus two groups can be recognized. The first group, for which we introduce the name *urna*-group, is characterized by the possession of a complex rosette, a usually large number of lateral ruffles, and spines of the *urna*-type. Species no. 2–6, including *Gyrocotyle major*, belong to this group. The second group, which we call *confusa*-group, is characterized by the possession of a simple rosette, a small number of lateral undulations and spines of the *confusa*-type. Species no. 7–10, including *Gyrocotyle abyssicola*, belong to this group.

Four of the host species are infested by two species of the subgenus *Amphiptyches*, one of each group. Two species of parasites that occur in the same host species have certain characters in common, especially characters of a quantitative nature, which shows that the gross morphology of a species is in general more similar to that of the other species from the same host, than to that of other species of the same group. Most probably this concerns adaptations to the host, although they cannot easily be understood, with the exception of the rule that large host species have large *Gyrocotyle* species.

The two new species also show this phenomenon. Most remarkable is their large size. Until now, the largest known species of the subgenus was *G. maxima*, which may have a length of up to 116 mm (Mendívil-Herrera, 1946). Both *Hydrolagus affinis* and *Callorhinchus callorhynchus* are relatively large host species. Both species differ from all other known species in that the receptaculum seminis is located in the middle of the body. In all other known species it is much closer to the tail region.

Gyrocotyle major is unique in that it has numerous very small spines on the base of the rosette and even extending to the anterior part of its plications. It differs from *G. fimbriata* in that the lateral ruffles do not extend to the funnel region, in the distribution of the body spines, in the larger size of the spines, in the more lateral position of the ♂ genital pore, in the absence of vitellaria in the funnel region, in the size and morphology of the eggs, and in the slightly different morphology of the larval hooks. *Gyrocotyle maxima* differs from *G. major* in that it has a wider uterine region, in the much smaller spines, and in the presence of larvae in the freshly laid eggs. A comparison with the other species of the *urna*-group is not yet possible because of the absence of adequate descriptions. *Gyrocotyle urna* is a small species quite similar to *G. fimbriata*. *Gyrocotyle nigrosetosa* is a larger species that is apparently closely related to *G. major*. Until now it has been found only twice (Haswell, 1902, Yamaguti, 1934), and it has been described only vaguely. In this species the ♂ genital pore is located slightly to the right of the median line. The eggs are rather small (80–90 × 60–70 μ) and thick shelled.

Gyrocotyle abyssicola differs from species no. 9, the only described species of the *confusa*-group, in the larger number of acetabular spines, in the distribution of the body spines, the larger fields of testis follicles, the presence of vitellaria in the funnel region, and the size and morphology of the eggs.

Some Morphological Characters

The spines. — The different categories of spines, viz., acetabular spines, body spines, and rosette spines, are recognized only for practical reasons. Basically these spines do not differ, and the different groups may merge with one another. However, there is an important difference between the spines of the two species. There is a great individual variability but nevertheless, in our experience, the two types can always be recognized. The same seems to hold for all species from other hosts and therefore we may speak of *urna*-type spines and *confusa*-type spines.

In spines of the *confusa*-type (Fig. 21 and 23), the basal part is the widest part of the spine and the distal part is generally slender and pointed. In general the shape is regular and symmetrical.

In spines of the *urna*-type (Fig. 20, 22, 24, and 25), the widest part lies at some distance distal to the basal part and there is often an evident constriction between these two parts. The distal portion of the spine is stouter and blunt. In spines of comparable dimensions, the points that protrude out of the skin are twice as wide in *G. major* as in *G. abyssicola* which is even striking when specimens are studied under a low-power stereomicroscope. The general shape is often irregular and asymmetrical.

In describing the acetabular spines, Lynch (1945) remarks that in *G. fimbriata* their shape is stubby, much like a tenpin, but often asymmetrical or clublike, and in species no. 9 graceful and symmetrical.

The shape of the spines is of the utmost importance for the identification of small specimens (post-larvae or ♂-mature specimens), because they already

have fully developed spines, but most other specific characters cannot yet be observed.

The ♂ genital pore. — This pore is located farther away from the median line in *G. major* than in *G. abyssicola*. This character can even be used when the ♂ pore is completely invisible, because the shape of the ventral field which is devoid of vitellaria is influenced by the location of the pore (compare Fig. 8 and 10).

The terminal genital ducts. — The shape, length, and relative length of the ejaculatory duct and the vagina provide important characters. Therefore, it is to be regretted that these organs could not properly be studied. Only the ♂-mature specimens of *G. major* provided some information. In this species both ducts are rather long and of approximately equal length (Fig. 26); both are winding and not straight as in some other species.

The term vagina is used here only to indicate the thickened anterior part of the duct from the vaginal pore to the receptaculum seminis. The long, thin-walled posterior part is called here vaginal duct.

The vitellaria. — The distribution of the vitellaria should be compared only in specimens of average or great dimensions, since they may be incompletely developed in smaller specimens. *Gyrocotyle abyssicola* differs from *G. major* in that a more efficient use is made of the available space: the follicles are more crowded, they envelop the acetabulum more closely, they occupy the whole region dorsal to the genital organs, and they extend to the funnel region.

The eggs. — The dimensions of the eggs of the two species largely overlap, but the average length is significantly greater in *G. major*, which results in a higher average length/width ratio. In fact there is only a small overlap, as may be concluded from Fig. 31. It is not possible to recognize each individual egg with certainty but a group of eggs can certainly be determined specifically, the more so since the eggs of *G. major* (Fig. 29) are generally less bluntly rounded, somewhat spindle shaped. The shell is slightly thicker in *G. major*.

Lynch (1945) observed the same difference in the shape of the eggs of the species from *Hydrolagus colliei*. However, in that case the species of the *confusa*-group has eggs that are "shaped more like a Rugby football."

The eggs of the species studied by Lynch (1945) were surrounded by a transparent jelly, 5.5–12 μ thick. Such a layer was not found in the eggs of the new species but it should be remarked that eggs of *G. major* that had been treated with methyl benzoate had a thick shell, 4–5 μ, with a transparent outer layer. Apparently the shell is capable of swelling.

The ♂-mature and ♀-mature stages. — Small specimens of *Gyrocotyle* in which the rosette and the lateral ruffles have not yet developed, are usually called postlarvae, juveniles, or immature specimens. However, the male organs may be completely developed already at an early stage. It is incorrect to call such specimens immature or juvenile. Therefore we propose to recognize a ♂-mature stage. This can be defined as the stage in which the sperm production has started, as is evident from the presence of sperm in the vas

deferens. The ♀-mature stage can be defined as the stage in which eggs are present in the uterus.

The receptaculum seminis may contain sperm in very small specimens but in our material this was probably not the case.

We may conclude that gyrocotylids are protandrous which is a quite common phenomenon in flatworms.

The larval hooks. — These hooks can be seen only in the ♂-mature stage but they may well be present in the ♀-mature stage too. The hooks are embedded in the wall of the anterior part of the funnel, forming a complete circle around the funnel. This suggests that the funnel originates from the centre of the former larval haptor. However, this does not conform to the observations of Lynch (1945) who states that the hooks are located on the dorsal wall of the funnel.

Lack of Species Intermingling

The lack of occurrence of *G. major* and *G. abyssicola* in the same host fish, *H. affinis*, is similar to the report by Lynch (1945) for the host *H. colliei* for which in 143 specimens infested with *Gyrocotyle*, 104 had *G. fimbriata* only, 36 had *G. urna* only, and only 3 possessed both *G. fimbriata* and *G. urna*.

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Increase in Aggression and in Strength of the Social Hierarchy among Juvenile Atlantic Salmon Deprived of Food[1]

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ABSTRACT

Aggressive behaviour of Atlantic salmon (*Salmo salar*) parr, tested in groups of eight, was greater during 3 days of deprivation of food than during 3 days of feeding. Frontal and lateral displaying appeared to increase more than charging and nipping. Increased agression was only partly a result of increased locomotion, and therefore was partly a direct effect of hunger.

Strong social hierarchies developed, larger fish nipping smaller ones more than the reverse. The correlation between size and hierarchical status was usually sufficient to account for the strength of hierarchy observed.

Upon deprivation of food the dominant of any pair of socially unequal fish on the average increased its nipping of the subordinate. The nipping rate of dominants by subordinates did not change consistently; many low ranking fish decreased their nipping rate upon deprivation. These results would strengthen hierarchies during deprivation. Initiation of attacks by small fish, as opposed to nipping, increased consistently during deprivation.

Nipping was more frequent between fish of equal status and size than between fish of unequal status or size. This could have accounted for the strength of hierarchies in groups in which the correlation between size and position was insufficient to do so.

The increase in aggression upon food deprivation could function to increase the size of feeding territories when food is scarce. This and the strengthening of hierarchies would cause emigration of some fish from the area. Concentration of aggression between fish of equal size and status could permit parr of different ages to coexist.

INTRODUCTION

If the function of territorial behaviour of young Atlantic salmon (*Salmo salar*) is to space the fish through the environment in such a way as to ensure efficient utilization of available food, the size of territories should increase when food is scarce and decrease when food is abundant. Such changes in territorial size would be brought about by appropriate increases and decreases in aggression. Laboratory experiments were designed to discover if food deprivation did or did not increase aggression among groups of young salmon in aquaria.

The effect of food deprivation on aggressive behaviour of juvenile Atlantic salmon was investigated earlier by Keenleyside and Yamamoto (1962). They found that aggression decreased after a week without food. However, they also showed that aggression increased among young salmon for as long as 40 min after feeding (fig. 11 of Keenleyside and Yamamoto, 1962) and

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their observations on fed groups, with which deprived groups were compared, were begun only 30 min after feeding. Also, prolonged deprivation of food must eventually cause weakness and a decrease of all activities of the fish. Though fish can live for much longer than a week without food (Brown, 1957), behavioural adaptation to starvation, such as a decrease in movement to conserve energy, may start within that period. The present work was planned to decrease the possibility of influence from both these factors by observing aggression of fed fish 13 hr or more after the latest feeding and by using deprivation periods of less than a week.

MATERIALS AND GENERAL METHODS

The Fish and Their Holding Conditions

Young salmon (parr) were obtained from the hatchery operated by the Department of Fisheries of Canada, Saint John, New Brunswick. The fish were kept in the laboratory for 1–6 months in circular, fibreglass holding tanks, 1 m in diam. They were measured shortly after they were obtained (Table I).

Table I. Numbers and lengths of the two lots of hatchery fish.

Date obtained (1966)	Dates used in expt.	No. of fish	Fork length (*cm*)	
			Mode	Mean
Jan. May	May 31–Aug. 25	26 141	6.4	6.6±2.6[a]
July	Sept. 30–Nov. 3	135	12.2	12.2±1.7[a]

[a]Standard deviation of mean.

Each fish was "cold-branded" with an individual number. Cold-branding (Everest and Edmundson, 1967) was performed with a tool described by Groves and Novotny (1965). The number remained distinguishable for 2 months under the temperatures (9.5–17.5 C) and feeding regime of the experiment.

A day–night light cycle of 18 hr light was maintained throughout the period of observations.

Experimental Conditions

Observations were made on groups of eight fish kept in rectangular experimental aquaria, each 100 × 40 cm. A group size of eight was chosen because Keenleyside and Yamamoto (1962) found that the maximum number of nips occurred in groups of about 8–10 fish in aquaria of approximately this size. Though the density was much higher than in nature, and the aquaria

were too small to allow the development of even one full-sized territory, each fish did have its individual resting spot, and aggression in the groups was common.

Water depth in the aquaria was kept to 15 cm. Sufficient water entered an aquarium to create a slow current from one end of the aquarium to the other. This current was strong enough to align the fish, and keep the floor of the aquarium clean of most excess food and faeces, but it was not strong enough to cause the parr to use their pectoral fins as planes for holding themselves to the bottom as had been described by Kalleberg (1958). Four or five fist-sized rocks were scattered about in each tank to provide some visual isolation and possible reference points for resting spots, but the bottoms of the aquaria were otherwise left bare to facilitate cleaning.

Cardboard screens were always kept in front of experimental aquaria except when the experimenter was cleaning the aquaria, replacing fish, or adjusting the activity recorder (description below). Observations were made through slots cut in the cardboard, and although fish could detect movement on the observer's side of the screen they did not appear to be disturbed by it. Without screening, the activity of the fish was easily disturbed by movement of people in the room.

Ground raw beef liver was fed to the fish with minimal disturbance by freezing a small quantity of liver into an ice cube in an ordinary refrigerator tray, and sliding this cube down a chute which projected from the observer's side of the cardboard screen to a soap dish in the aquarium. The cube melted completely, releasing the food, in about 15 min.

Experimental Procedure

The basis of the experiment was the comparison of behaviour of each group of eight fish during 3 days of feeding to excess with their behaviour during 3 days of deprivation. Deprivation or feeding periods for each group were interspersed randomly either until a statistically significant difference between total numbers of nips under the two conditions occurred (using a Mann-Whitney U-test (Siegel, 1956) on the averages of daily totals of 3-day periods), or until one of the fish died. When one died the remaining fish were discarded and a new group was introduced to that aquarium. Randomization of feeding and deprivation periods prevented irrelevant behavioural changes, arising possibly from seasonal temperature changes or from continued acquaintance of the fish with each other or their surroundings, from causing a consistent bias in the results.

Each group of eight fish was introduced to an aquarium and given at least one 3-day cycle under normal feeding conditions to settle down before observations were begun. Details of the procedure during the 3-day cycle follow.

First and second days: Each group of fish was observed for 10 min each day. These observations were always made between 0900 and 1000 hr. At 1030 hr (or immediately after observations on weekends) those groups which

were not being deprived of food were fed. A second feeding occurred at 1630 (or until as late as 2000 hr on weekends). Thus there was always at least 13 hr between the morning observation period and the nearest previous feeding.

To establish correlations between activity and aggression, additional data were needed. Therefore, some observations on aggression of groups in aquaria equipped with activity recorders were made before the afternoon feedings. Data from these afternoon observations were not used in any other part of the study.

Third day: All groups of fish were fed after the morning observations. At approximately 1500 hr excess food and faeces were siphoned from the aquaria. Then a feeding or deprivation treatment was randomly assigned to each group of fish for the next 3-day cycle. Thus fish not fed on consecutive cycles still received a meal every 3rd day, and, in addition, by the time observations were made on the first day of the cycle those groups being deprived had already been without food 5–10 hr longer than those being fed.

No consistent increases or decreases in aggression between cycles could be shown later by examination of data from groups that underwent three or more consecutive 3-day deprivation cycles. The single feeding between cycles therefore seemed to have been sufficient to prevent weakness from hunger from influencing results.

Behaviour Recorded

Locomotor activity was recorded in two aquaria, each equipped with three photoelectric cells coupled to an event recorder. An event was recorded each time a fish moved into a light beam. A disadvantage of this system was that shifts in individuals' resting sites, and resultant changes in patterns of movements of fish through the aquaria, caused high variability in the recording, making comparisons between 3-day cycles difficult. Even so, certain trends in the activity counts could be observed (Fig. 1), and the increase in activity counts after feeding agreed with my subjective impressions of activity changes, and with the results of Keenleyside and Yamamoto (1962).

The following five aggressive behaviour patterns described by Keenleyside and Yamamoto (1962) were also observed and recorded: charging, nipping, chasing, frontal display, lateral display. In addition "approaches," distinguished from "charges" by slow speed, were recorded. Both charging and approaching involve visual fixation of approached fish, unlike chance approach during feeding or ordinary locomotion. So far as was possible, the attacker and attacked were identified by their numbers in the written recording.

Initiation of attacks was also used as a measure of aggression. Initiation of an attack was defined as any approach or charge whether or not the approach or charge was followed by displaying, nipping, or chasing, so long as that approach was not a direct retaliation to an immediately preceding attack by the approached fish. Sometimes lateral displaying occurred without movement towards the recipient fish; so long as this was not retaliatory it was also counted as initiation of an attack. Because this measure included movements too

incomplete to be classified as charging, displaying, etc., it was considered to be the most sensitive measure of incipient aggression.

INCREASE IN FREQUENCY OF AGGRESSIVE ACTS DURING FOOD DEPRIVATION

Of 13 groups of fish tested, 12 showed greater mean numbers of all aggressive acts during periods of deprivation than of feeding ($P < 0.02$, Table II). Within each of three groups by themselves the number of all aggressive acts was greater ($P \leq 0.05$) when the fish were not fed than when they were.

TABLE II. Mean numbers of all aggressive acts in 10 min for all groups when fed for 3 days and when not fed for 3 days.

Group[a]	No. of 3-day cycles		Mean of all aggressive acts by eight fish in 10 min		Probability within group of difference arising by chance (Mann-Whitney U-test)
	Not fed	Fed	Not fed	Fed	
a	7	12	26	23	>.10
b	7	8	26	18	.15
c	10	5	29	20	>.10
d	9	4	38	9	<.02*[b]
e	4	8	36	21	.13
f	5	3	12	2	.04*
g	9	4	9	29	>.10
h	5	4	21	10	.06
i	4	6	32	12	.17
j	7	3	28	6	.02*
k	2	4	19	14	.80
l	3	2	39	25	1.0
m	8	5	17	7	.1

[a]For all groups: T = 10.5; $0.01 < P < 0.02$ (Wilcoxon matched-pairs signed-ranks test; Siegel, 1956).

[b]*Significant at $P < 0.05$.

There seemed little doubt that a 3-day deprivation of food caused an increase in the total number of all acts of aggression.

This increase upon deprivation held true for each of the individual types of aggressive acts. When each type was treated in the same manner as was the total of all acts of aggression (Table III), all five types occurred more frequently under deprivation conditions in almost all groups ($P < 0.02$). The number of groups out of 13 in which the difference was statistically significant within groups by themselves ranged from one to five for the different acts. Frontal displaying increased reliably ($P < 0.05$) in more groups than any other type of act; chasing showed significant increases in the fewest groups (Mann-Whitney U-test).

TABLE III. Effects of food deprivation on different aggressive behaviour patterns.

Behaviour pattern	Probability over all 13 groups that change in frequency of act upon deprivation of food arose by chance[a]	No. of groups out of 13 in which the no. of acts increased significantly ($P < .05$, Mann-Whitney U-test) when fish were deprived of food	Mean no. of each behaviour pattern/10 min for all groups when fed	Mean % increase when fish were deprived of food
Frontal display	$<.01$	5	55.1	87
Lateral display	$<.02 > .01$	2	36.9	77
Charging	.02	2	49.0	55
Nipping	$<.02 > .01$	2	48.7	43
Chasing	<0.1	1	12.1	102

[a]Wilcoxon matched-pairs signed-ranks tests.

Food deprivation probably did not cause equal increases in the various acts of aggression. Although the percentage increase was greatest for chasing (Table III), the figure given is unreliable because of the low numbers of this act observed when fish were fed. (It was less than one third as frequent as any other act.) This unreliability is also reflected in the low numbers of groups (only one) which showed a significant increase in chasing when the groups were deprived of food. Of the other acts, frontal displaying increased most, followed by lateral displaying, then charging, and finally nipping. The difference in percentage increase between frontal threatening and nipping was significant only at $P = 0.1$ (Wilcoxon matched-pairs signed-ranks test).

RELATION BETWEEN ACTIVITY AND AGGRESSION

The analysis of the previous section does not indicate whether the observed increase in aggression was a direct or indirect result of food deprivation: as the fish increased their search for food, locomotor activity may have increased, and such an increase in locomotion would be expected to increase aggression as a result of fish more frequently coming into close proximity with one another. Activity records (Fig. 1) seem to indicate that at least in the morning (0400–1000 hr) locomotion may indeed have been higher when fish were deprived of food. Since observations were made within this time period, a further analysis was necessary if a direct effect of food deprivation on aggression was to be shown.

If food deprivation had a direct effect on aggression, more aggression should have occurred at a given activity level when the fish were deprived of food than when they were fed, assuming that the patterns of locomotion of fish about the aquarium remained similar under the two conditions. No

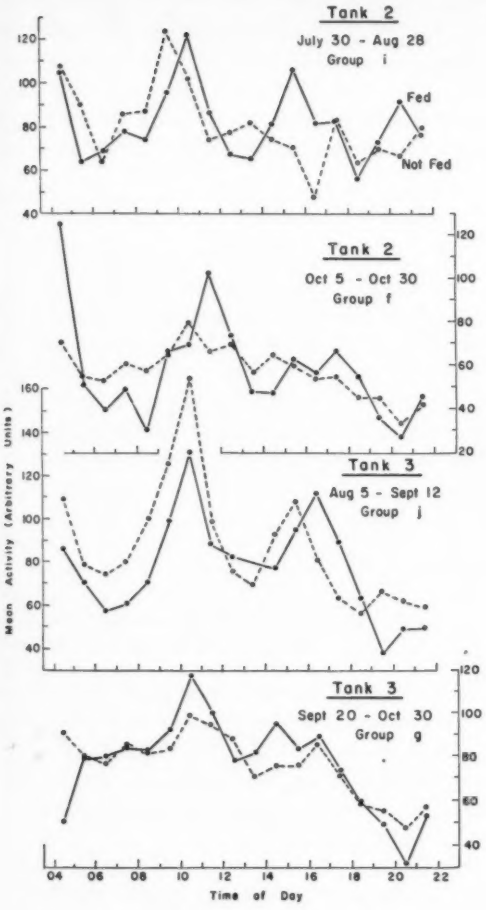

FIG. 1. Averages, from daily activity recordings, of all hourly counts of events for four groups of fish when fed and when not fed. Number of observations for any one point ranged from 4 to 26. Feedings took place between 0930 and 1030 hr, and between 1630 and 2000 hr.

reason for rejecting the assumption could be seen. To make the comparison the 10-min observation periods were classed according to the number of activity events when the fish were deprived of food and when they were fed. Then the average number of aggressive acts was calculated for each activity class, lumping morning and afternoon observations since these could not be found to differ. This was done for each of the five groups of fish whose activity was recorded.

For the four groups with the greatest numbers of comparable activity classes, most classes were observed to have higher numbers of aggressive acts when fish were deprived of food than when fed (Fig. 2). If the differences in aggression already found during the fed and not fed conditions were caused by differing activity, classing observations according to activity level could cause this effect of deprivation to disappear, but could scarcely reverse it.

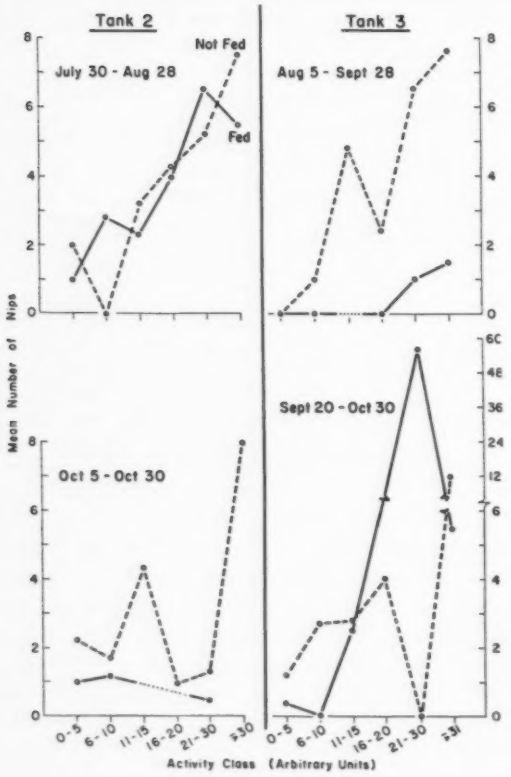

FIG. 2. Mean numbers of nips/10 min by all eight fish when fed and when not fed for various classes of locomotor activity. Data from four groups out of five, of eight fish each, with the greatest numbers of comparable observations. The numbers of observations from which means were calculated are:

Activity class:	0–5	6–10	11–15	16–20	21–30	31
Tank 2 July–Aug.						
When not fed:	2	3	5	3	4	2
When fed:	6	4	4	4	4	2
Oct.						
When not fed:	5	6	3	2	6	1
When fed:	5	4	0	0	2	0
Tank 3 Aug.–Sept.						
When not fed:	2	3	4	5	6	6
When fed:	6	3	0	1	3	2
Sept.–Oct.						
When not fed:	18	10	5	2	1	4
When fed:	9	1	2	0	2	1

Therefore the null hypothesis (H_0) was that aggression was not increased by deprivation. This hypothesis could be rejected ($N = 5$, $x = 0$, $P = 0.031$, one-tailed sign test), and therefore aggression was increased directly by food deprivation, apart from or in addition to indirect increases resulting from possibly greater locomotion during deprivation.

INDIVIDUAL CHANGES IN AGGRESSION

To find out if the increase in total aggression could be attributed to increases made by just a few of the eight fish in each tank, a preliminary analysis was made comparing the numbers of fish which initiated attacks (regardless of whether or not these attacks were completed) under each of the two conditions. In all but 3 of the 13 groups of fish the mean number of individuals initiating attacks was higher ($P < 0.05 > 0.01$; Wilcoxon matched-pairs signed-ranks test) when they were deprived of food than when fed. The mean numbers of individuals initiating attacks in the 13 groups under the two conditions were:

Group:	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*
Not fed	5.1	6.4	6.7	6.9	5.4	3.8	3.9	4.8	6.3	4.0	7.1	6.0	4.8
Fed	5.8	4.9	5.6	4.8	3.6	3.0	2.5	3.5	5.9	4.8	6.6	7.0	3.7

This increase in number of aggressive individuals was shown to be due to an increase in the percentage of smaller fish initiating attacks when they were not fed. When the fish in each of seven groups (those in which brand numbers were clearly distinguishable for most of the observations) were divided into four small and four large fish, most of the larger fish were usually found to be initiating (and possibly completing) attacks whether they were being fed or not (Table IV). Among the four smaller fish, however, more initiated attacks when deprived of food than when fed ($T = 2$, $P = 0.05$, Wilcoxon matched-pairs signed-ranks test, Table IV).

If population density was decreased and territory size increased through displacement of weaker fish when food was scarce, the behavioural difference between stronger and weaker fish should have been enhanced by food deprivation. Such enhancement of differences is not evident from the foregoing analysis for two possible reasons: (1) the relative aggressiveness of different individuals was not measured, but was assumed by implication to be related to size, which was not necessarily true; and (2) while small fish initiated more attacks than large fish during deprivation, emigration would be more likely to follow defeat in a battle in which nipping rather than mere approaching was prominent. The following analysis of social structure was therefore carried out using nipping behaviour as a means of ordering fish in a social hierarchy. The relation of size to rank in the hierarchy and effect of food deprivation on the strength of the hierarchy are examined.

TABLE IV. Mean percentages of four small and four large fish, in the seven groups examined, which initiated attacks during feeding and deprivation cycles. For number of cycles at each condition for each group see Table I.

Group	Small fish		Large fish	
	When fed	When not fed	When fed	When not fed
a	56	70	81	75
b	44	57	78	79
c	80	72	75	93
d	50	80	75	95
e	78	69	78	88
f	17	30	67	65
g	50	72	19	19

THE SOCIAL HIERARCHY AND ITS DEPENDENCE ON SIZE

The structure of most groups in these small aquaria approached a perfect hierarchy when measured according to the criteria of Landau (1951a). Measurement was in terms of "*h*," the hierarchy index, which could vary between 0 and 1, 0 representing a social group with maximum equality, and 1 representing a group in which there was a perfect hierarchy. The value of *h* was calculated from the formula (Landau, 1951a):

$$h = \frac{12}{n^3 - n} \sum_{j=1}^{n} (V_j - \frac{n-1}{2})^2$$

where n is the number of fish in the group, and V_j is the number of pairs in which the jth fish nipped the fish with which it paired more than it was nipped by that other fish. Interactions in some groups (particularly group *f*, Table V) were not observed between all possible pairs, and sometimes ties occurred in numbers of nips made by the two fish. Both these conditions preclude the use of the formula, and therefore 7 of the 13 groups had to be excluded from the analysis because too few pairs interacted. Where no interaction or ties occurred in the remaining six groups, an arbitrary decision was made as to which fish should be considered the dominant of the pair, provided that this decision reduced the value of *h* in cases where the value of *h* was affected. Data for fish when fed and when not fed were combined in the calculation of *h* in order to obtain data on as many pairings as possible.

Perfect hierarchies were found in two of the groups and the lowest value among the six groups examined was 0.57 (Table V). If dominance between

TABLE V. Strengths of the nipping hierarchies observed, and the hierarchical strengths expected if size of fish were the only determinant, for the six groups for which data were sufficient for analysis.

Group	Hierarchical strength observed	Correlation between individual's size and position in hierarchy	Strength of hierarchy expected on basis of correlation of size with dominance	Mean no. nips/10 min evenly weighted (see text) for feeding and deprivation treatments
	h		*Expected h*	
a	0.57	+0.42	0.46	7.0
b	1.00	+0.95	1.00	4.1
c	0.71	+0.83	0.78	6.8
d	1.00	+0.83	0.80	5.8
e	0.62	+0.19	0.36	7.4
f	0.67	+0.79	0.69	1.7

pairs of fish was determined at random, the value of h would have been approximately 0.333 as can be calculated from Landau's (1951a) formula:

$$\text{expected } h = \frac{3}{n+1}.$$

Since every group exceeded this value there can be little doubt that fish were not reacting to one another at random, but nipped some fish consistently more frequently than they nipped others.

The effect of size of fish on the strength of the hierarchy could be examined through use of another formula of Landau (1951a), which makes use of the correlation between the sizes of the fish and their positions in the hierarchy. The correlations for each of the six groups are given in Table V. If size alone were dictating positions of fish in the hierarchy, according to Landau (1951a)

$$\text{expected } h = \frac{3}{n+1} + \frac{n-2}{n+1} h_a.$$

The value of h_a is dependent on "r" the correlation coefficient, and can be read from fig. 2 of Landau's (1951a) paper. With the exception of groups *d* and *e*, the values of h expected from the correlation between size and hierarchical position approximate the values observed (Table V). These results indicate that though some additional factors (see below) may further strengthen the hierarchy, difference in size of fish in most groups was sufficient to account for the degree of hierarchical organization found.

Although the hierarchical organization of groups means that fish of low rank generally receive more nips than those of higher rank, the greatest exchange of nips tends to occur between fish of nearly equal rank rather than between fish of widely differing rank. In these groups rank could range from one to eight, and the size of the difference in rank correlated negatively with the mean number of nips exchanged by pairs in all but one group:

Group:	*a*	*b*	*c*	*d*	*e*	*f*
r_s	+0.28	−0.68	−0.80	−0.86	−0.43	−0.30

Some of the correlations are low (e.g., −0.30) but if they reflect the true relationship between fish, the value of *h* should also be negatively correlated with the number of nips made by the entire group of fish, since when *h* is low the fish are more nearly equally ranked. The values of *h* and mean numbers of nips/cycle (calculated as the mean of the two means for feeding and deprivation cycles thereby giving equal weight to the various treatments in groups which had more cycles of one treatment than the other) are given in Table V. The fish of group *f* (and *g*) were obtained in July (Table I) and for some unknown reason displayed significantly less aggression when deprived of food than all other groups ($P = 0.05$, Mann-Whitney U-test). Therefore, only groups *a*–*e*, observations on all of which were begun on the same day, were used in the calculation of the coefficient of correlation between *h* and absolute numbers of nips. A negative correlation of −0.87 was found, substantiating the conclusion that aggression was greater among fish of nearly equal rank.

Because position in the hierarchy depends on size, nipping ought also to be greater within pairs of fish of nearly equal size than within pairs differing more in size. Fish of each group were ranked from smallest to largest, and fish adjacent in the rank or separated by only one intervening fish were designated "equally sized," and pairs with two or more intervening fish were designated "unequally sized." For all six groups the mean number of nips per pair per 30 min (weighted evenly as above for deprivation and feeding treatments) was greater when fish were of approximately equal size (Table VI).

TABLE VI. Mean numbers of nips/30 min within pairs of equally and unequally sized fish in six groups for which data were sufficient for analysis.

Group:	*a*	*b*	*c*	*d*	*e*	*f*
Pairs equally sized	0.81	0.37	1.13	0.78	0.75	0.37
Pairs unequally sized	0.57	0.35	0.39	0.46	0.74	0.18

STRENGTHENING OF HIERARCHY BY FOOD DEPRIVATION

Not all fish increased their nipping upon deprivation of food. In the six groups studied, 28 fish increased nipping during deprivation, but 20 decreased or made no change in nipping. Of those that decreased or remained unchanged, 15 ranked low in the hierarchy ($V_j \leq 3$) whereas only five were high ranking fish ($\chi^2 = 3.62$, $.05 < P < .10$).

Reception of nips by subordinates also increased in relation to those received by dominants during deprivation (Table VII). In all but one of

TABLE VII. Percent increase in nips within pairs during 30 min by fish higher in hierarchy to those lower, and by those lower to those higher, when deprived of food in six groups of fish for which data were sufficient for analysis.

Group	Mean no. of nips by higher ranking to lower ranking fish when fed	% increase when not fed	Mean no. of nips by lower ranking to higher ranking fish when fed	% increase when not fed
a	0.49	+108	0.16	−44
b	0.31	+3	0.10	−60
c	0.83	+10	0.06	+280
d	0.39	+118	0.09	+62
e	0.62	+55	0.01	0
f	0.50	+26	0.05	+20

the six groups (group *c*) the dominants increased nips to subordinates more than subordinates increased nips to dominants. In fact, in some groups subordinates on the average decreased the number of nips they made to dominants when deprived of food. Thus, in general, deprivation of food increased the strength of the hierarchy. (There were too few data to permit separate calculations of *h* under each condition.)

DISCUSSION

A possible behavioural mechanism for regulating population density of Atlantic salmon parr according to the availability of food has been indicated by the results of this experiment. The increase in nips delivered by dominant fish to those lower in the hierarchy when the fish were not fed may be an expression of an attempt to increase territorial size, and in any case would tend to disperse fish that otherwise might inhabit the same area. Chapman (1962) showed that aggression can cause emigration of juvenile coho salmon from a stream channel. Also, Mason and Chapman (1965) using two stream channels from which fish could emigrate at will, showed that the channel which had greater natural drift food supported, over 4 months, 63% more

fish than did the channel with less food. To hypothesize that the increased aggression that occurred among juvenile Atlantic salmon upon deprivation of food would cause emigration of low ranking fish seems reasonable.

Magnuson (1962) in a set of excellent experiments showed similar changes in the aggressive behaviour of medaka (*Oryzias latipes*) when food was limited. Well-fed, large, dominant fish were less aggressive than large dominants whose food was limited. In contrast to Atlantic salmon, small medaka were all unaggressive whether or not food was limited or present in excess. Magnuson pointed out that the advantage (measured as growth rate) of social dominance was great only when food was concentrated in one area and visual isolation between competitors was extensive.

Food deprivation probably increases the probability within every salmon parr of performing an aggressive act, but the type of aggression performed differs according to rank and relative size of the fish. Smaller, and therefore usually subordinate, fish may initiate more attacks when deprived of food than when fed, but they may actually decrease nipping behaviour. The greatest increases in nipping are made usually by the larger, dominant fish. In view of this, the total number of nips by a group of fish is not a good measure of the influence that some factor such as starvation has on individual aggression.

Display behaviour probably is the type of aggression increased most by food deprivation, particularly frontal displaying. Display behaviour is also likely to be the least costly in energy requirements of all aggressive behaviour patterns (nipping is usually preceded by charging or chasing, both of which must require much energy). Therefore the proportionately greater increase in displaying seems to be adaptive to the species.

A tendency to concentrate nipping between fish of nearly equal size and rank would allow differently aged salmon parr (migration to the sea may occur as late as 4 years after hatching (Saunders, 1967)) to inhabit the same area. In rivers and in a stream channel I have observed small fish living between or on the peripheries of the territories of larger parr. Since differently sized fish are likely to require different food, behaviour which focuses competition for space on fish of similar sizes could also be adaptive.

Landau (1951b) points out that factors which restrict challenges or which restrict reversals of dominance to pairs of fish of approximately equal rank could cause nearly perfect hierarchies in societies where other factors are insufficient to do so. Though the correlation between size and rank was sufficient to account for the strength of hierarchical organization observed in most groups, size alone appears to have been insufficient at least in one group (*e*), and possibly in others (*d* and *a*). The concentration of nipping within pairs of nearly equally ranked fish seems to fulfil the requirements for development of hierarchies of the strengths observed. In streams the hierarchy would be further strengthened if the loser of a contest between two similarly sized, similarly ranked individuals left the area. Emigration of one of any pair of equal fish would result in the remaining individuals forming a group of dis-

tinctly sized and ranked fish capable of utilizing every niche in the environment most suited to such differently sized fish.

Behavioural reaction to food shortage by salmon parr, therefore, may adapt them to their habitat by causing expansion in territorial sizes and strengthening of hierarchical organization. In pools, coho salmon (Chapman, 1962) and brook trout (Keenleyside, 1962) form less distinct territories than in riffles, and coho may even develop loose social hierarchies. Atlantic salmon parr may not be as social as these species under natural conditions (Keenleyside, 1962), but if partial territories are permitted (a partial territory being an area defended against all but those superior to the defendant in rank), food deprivation would strengthen the hierarchical structure of the territorial society. Both adaptive changes could take place through the increases in aggression during food deprivation demonstrated in this paper, and both changes should cause emigration of some of the fish. Apparently, not always the smallest fish should emigrate, which if true, would help to ensure survival of some parr from each year-class present in the area.

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Some Morphological and Biochemical Changes in Coho Salmon, *Oncorhynchus kisutch*, During Parr–Smolt Transformation[1]

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ABSTRACT

Growth rates and changes in some chemical constituents were investigated in laboratory-reared and wild coho salmon in the pre-smolt, smolting, and early post-smolt stages of their life cycles.

Laboratory-reared pre-smolts of coho salmon continued to grow during fall and early winter but at an ever diminishing rate. During late winter, spring, and early summer, growth in both length and weight of these fish was exponential with time. In wild coho pre-smolts there was no apparent winter growth but, with the onset of warmer waters and longer day lengths in the spring, growth in both length and weight became exponential with time. Exponential growth continued in wild post-smolts held in seawater pens but at a slower rate than during smolting.

It is postulated that the power b in the weight–length formula $W = aL^b$ is approximately 3.2 and that during smolting, when the fish are becoming more streamlined, the parameter a decreases from approximately 7.5 to about 6.2.

Guanine levels in belly skin, which appeared to be related to lighting conditions and physiological state of the fish rather than to length or weight, increased during smolting to about 6 $\mu g/mm^2$ skin and remained at these levels.

In pre-smolt laboratory-reared fish total lipid increased with increasing growth. With further weight increases during exponential growth, the weight of lipid remained relatively constant and the amount of lipid per unit weight decreased. A decrease in percent lipid did not occur in wild fish.

Total moisture, dry material, and nitrogen were linearly related to weight in the size-range investigated, but a sharp inflection in each least-square fit line occurred for moisture and dry material at a fish weight of 15 g and for total nitrogen at 7.5 g. These shifts in composition were related to fish size rather than to age, environment, or physiological state. During exponential growth, moisture, dry material, and nitrogen increased with increasing weight but whereas moisture increased at a slower rate than weight, solids and nitrogen increased more rapidly.

INTRODUCTION

First metamorphosis, or parr–smolt transformation, of young salmon prior to and during their seaward migration is accompanied by a slight change in form and by several histological, biochemical, physiological, and behavioral changes. These changes, which have been the subject of several reviews (Baggerman, 1960; Barrington, 1961; Hoar, 1965), produce a more streamlined fish better able to survive oceanic life. The present communication deals with growth and the changes in some chemical constituents of pre-smolt, smolting, and post-smolt coho salmon (*Oncorhynchus kisutch*) reared in captivity. A preliminary comparison between laboratory-reared and wild fish is also included.

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MATERIALS AND METOHDS

Three thousand hatchery-reared coho fry were transported from the Washington State Hatchery at Skykomish, July 9, 1964, to the Vancouver laboratory where they were placed in a circular stock tank 1.8 m in diam containing 5000 liters of water. The fish had been feeding for 101 days at this time. On July 20, 1400 fish were removed for other experiments; the remaining fish were designated N-1, and sampled at intervals until December 21. Thirty fish were removed on August 31, and marked by inserting a loop of nylon suture (monofilament, noncapillary, 00 guage) through the back musculature either anterior or posterior to the dorsal fin. Short lengths of variously coloured nylon threads were attached to the loops. These 30 fish were designated N-2, and transferred to an oval tank. Fourteen of this group survived with intact marks until the experiment was terminated by disease in June 1965. On January 12, 1965, the remaining N-1 fish were measured: 75 fish less than 8.5 cm in fork length were discarded; 125 fish between 8.5 and 10.5 cm were designated N-1A and placed in an oval tank; 235 fish greater than 10.5 cm were designated N-3 and distributed among three oval tanks, the remaining 648 fish, which were between 8.5 and 10.5 cm long, were used for other experiments. The oval tanks which measured 48 × 110 cm contained 225 liters of water.

During 1965 and 1966 wild pre-smolts and migrating smolts were obtained at intervals from the Big Qualicum River system on the east coast of Vancouver Island. The fish sampled on February 21 were overwintering among dead leaves and other debris in the water under the creek banks and had to be obtained by electrofishing. The fish sampled at other times were swimming freely. On May 25, 1966, some wild migrating smolts were transferred to pens placed in Deep Bay, 8 miles along the coast from the river mouth, and sampled at intervals until July 20. The range in salinity of Deep Bay water was 24.2–28.8‰ during the experimental period.

Aquarium lighting was completely artificial, and was provided by banks of fluorescent fixtures each containing a 48-inch 40-w daylight lamp[2] and a 48-inch 40-w "plant-gro" lamp[2] 8 ft above the water surface. The lighting system was activated by an astromic time switch[3] which was set for 45°N lat. The environmental conditions to which the fish were subjected are presented in Fig. 1.

All laboratory fish were reared in continuously flowing well-aerated water in which a water current was maintained by immersed sump pumps.[4] The laboratory fish and the wild fish in pens were fed once daily to satiation with a wet diet.[5] The fish in the pens may also have picked up additional feed from the water which flowed through the pens as a result of tidal action.

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[2]Models F40/D and F40/GRO obtained from Canadian Westinghouse Co.
[3]Model 72 20Z obtained from Tork Time Controls Inc., Mount Vernon, N.Y.
[4]Model 2-u 110 obtained from Little Giant Pump Co., Oklahoma City, Okla.
[5]Beef liver, 4500 g; beef heart, 4500 g; canned salmon, 4500 g; salt, 110 g; pablum, 40 g.

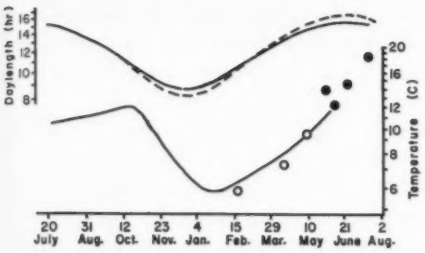

FIG. 1. Seasonal changes in photoperiod and temperature to which the fish were subjected. The solid lines represent laboratory conditions 1964/65; the broken line and circles represent field conditions 1965/66, the open circles representing Big Qualicum River temperatures and the solid circles seawater temperatures at Deep Bay.

Samples of laboratory fish were removed at intervals and anaesthetized immediately with 2-phenoxyethanol; fork lengths and live weights were recorded and subsamples of the N-1, N-1A, and N-3 groups taken for chemical and other analyses. Fish for analyses of total lipid and belly skin guanine were placed individually in small plastic bags, frozen on dry ice, and stored at −20 C for a few days until analyzed. Fish for moisture determination were placed in dried and tared aluminum dishes, and fish for total nitrogen analysis in acid-digested, large screw-top test tubes, prior to freezing. Moisture and nitrogen determinations were begun immediately after sampling the laboratory fish or on returning from the field. The balance of the anaesthetized fish were returned to their respective tanks, where they recovered in a few minutes. Big Qualicum River fish were transported to a laboratory adjacent to the river before being anaesthetized; the time between capture and anaesthetization was less than 30 min.

Each chemical analysis was performed on individual fish: total nitrogen by the Kjeldahl method (Association of Official Agricultural Chemists, 1960); total solids by drying to constant weight at 105 C; total moisture by the difference between live and dry weights; and total lipid by the method of Folch et al. (1957). Guanine was determined by digesting a rectangular section of belly skin (Markert and Vanstone, 1966) in N KOH for 24 hr at room temperature. The digest was filtered through glass wool to remove traces of lipid globules and scale skeletons, and stored at 0 C. Aliquots of each solution were applied to Whatman No. 40 paper, and the components separated by descending chromatography at room temperature for 24 hr using isopropanol:HCl:H_2O (170 ml: 41 ml, made to 250 ml) (Wyatt, 1955). After drying at room temperature the papers were examined under short-wave radiation (253.7 mμ) and the sections of paper containing guanine, and some hypoxanthine, were eluted with 0.1 N HCl. The volume of eluant was adjusted with 0.1 N HCl and guanine determined from its fluorescence at 340 mμ with an excitation at 285 mμ (Udenfriend and Zaltzman, 1962). These investigators found that hypoxanthine does not contribute to the fluorescence under these conditions.

The weight–length relation ($W = aL^b$),[6] lipid–weight relationship ($F = cW^d$),[6] and the moisture–, solids–, and nitrogen–weight relationships ($Y = e + fW$),[6] together with the type 2 errors of the parameters, were determined by the method of least square fit. Moisture, solids, and nitrogen in fish of the

mean weight at each sampling time were determined from the equations of the least-square fit lines of these components on weight. The resultant fitted values of these components and the mean values for length, weight, and guanine were plotted on a logarithmic basis against time ($\overline{Y} = gh^t$).[6]

During periods of exponential growth, or guanine deposition, the above plots against time formed relatively straight lines. Growth rates in length and weight, and the rates of increase in guanine, moisture, solids, and nitrogen, were determined from the slopes of the calculated least-square fit lines through these plots. Similarly, mean weight and fitted weights of moisture, solids, and nitrogen in wild fish at each sampling time were plotted against mean length on a log–log basis and the slopes, j, of the least-square fit lines calculated ($Y = i\bar{L}^j$).[6]

Since the N-1A population was from a selected group which was held in a different-sized tank at a different population density than the N-1 fish, the two groups are not comparable. However, for ease of presentation, they are shown together on the same graphs.

RESULTS AND DISCUSSION

Growth in Length and Weight

The transfer of fish from one tank size, or population density, to another resulted in growth curves for length and for weight which did not settle down to regular patterns for some time (Fig. 2). Thus the growth rates between the first and second samplings of the N-1, N-1A, and N-3 fish were less than those between the second and third samplings, whereas in N-2 fish the rates between the first and second samplings were greater. Similar findings have been reported by Brown (1957). The capture of wild migrating smolts and their transfer to holding pens in sea water resulted in a temporary cessation of growth which may have been a result of several causes such as adaptation to sea water, changed diet, crowding, and shock.

The laboratory-reared fish continued to grow during the summer, fall, and early winter but at an ever diminishing rate. Growth curves during these periods of the year resembled the latter portion of a sigmoid curve, as is characteristic of summer and fall growth of wild and hatchery-reared salmonids in fresh water (Ricker and Foerster, 1948; Fry, 1953; Kennedy, 1954; Salo and Bayliff, 1958; Allen, 1959; and Lawrie, 1963). As day length and temperature began to increase in late December and January, growth rates in these fish increased and became exponential with time. During this period of exponential growth, length increased 0.2% per day and weight increased 0.4–0.6% per day.

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[6]W = fish weight (g); L = fork length (cm); $\bar{L}$ = mean fork length (cm); F = weight of lipid (mg); Y = fitted weights of moisture, solids, or nitrogen (mg); $\overline{Y}$ = mean fork length (cm), mean weight (g), mean weight of guanine (μg), or fitted weight of moisture, solids, or nitrogen (mg); t = time (days); the lower case letters a–j are constants.

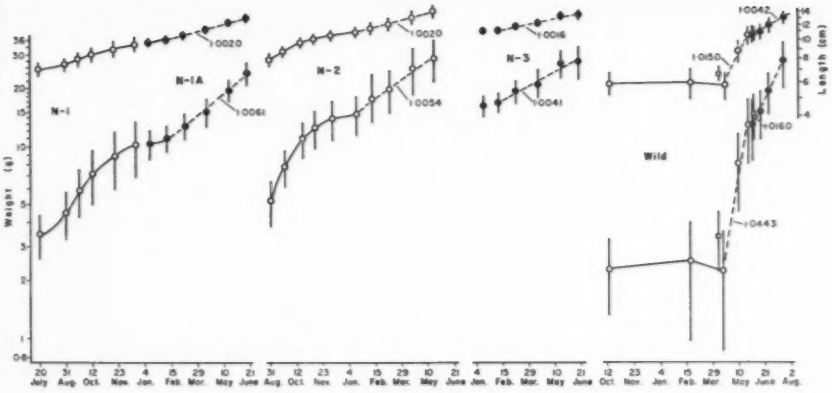

FIG. 2. Growth in mean fork length and in mean weight of six groups of juvenile coho salmon. The circles represent 1964/65 laboratory and 1965/66 Qualicum fish. The open circles represent N-1, N-2, and wild fish in fresh water. The solid circles represent N-1A and N-3 fish in fresh water and post-migrant wild fish confined to pens in sea water. The open squares (four) represent 1965 pre-migrant and migrating wild fish in fresh water. The broken lines represent the least-squares fit lines of length or weight on time, and the slopes of these lines are shown on the graphs. The vertical bars represent two standard deviations of each sample.

There was no apparent growth in length or weight of the wild fish from October 15, 1965 to April 14, 1966 but thereafter it became exponential with time. From April 14 to May 25, when the fish were actively migrating to sea, length increased 1.5% per day and weight increased 4.4% per day. Growth of these fish in pens in sea water remained exponential but at slower rates with length increasing 0.4% per day and weight increasing 1.6% per day. Whether or not the slower post-migrant growth rates of these fish are a normal occurrence is uncertain.

WEIGHT–LENGTH RELATIONSHIPS

With the exception of the initial N-1 sample, the plots of mean weight against mean length of fish not growing exponentially were very close to the upper broken lines in Fig. 3:

$$\log W = \log 7.486 + 3.2374 \log L.$$

The parameter b of the weight–length formula $W = aL^b$ for these samples was approximately 3.2 for the N-1 and wild fish and 3.4 for the limited number of N-2 fish (Table I).

During exponential growth in fresh water the fish became slimmer and had a more streamlined appearance, and the plots of mean weight against mean length approached and clustered around the lower broken lines in Fig. 3:

$$\log W = \log 6.2 + 3.2374 \log L.$$

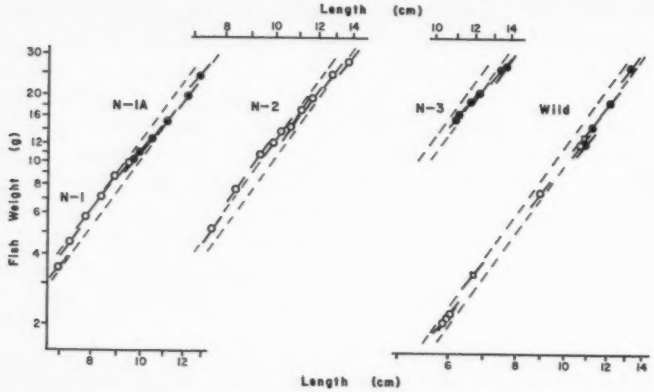

FIG. 3. Relationships of mean weight on mean fork length of six groups of juvenile coho salmon with a section of least-square fit line of weight on length for each sample. The symbols are the same as those used in Fig. 2. The upper broken line of each graph represents the average least-square fit line of weight on length of the September, October, and November N-1 samples; log weight, mg = log 7.486 + 3.2374 log length, cm (a = 1/272 [(57 × 10.35) + (124 × 6.29) + (91 × 7.29)] = 7.486 mg; b = 1/272 [(57 × 3.07622) + (124 × 3.30836) + (91 × 3.24166)] = 3.2374). The lower broken line on each graph is included for reference purposes and its equation is: log weight, mg = log 6.2 + 3.2374 log length, cm.

The parameter b of individual samples approximated 3.0 in N-1A and N-3 fish and 2.8–3.0 in wild fish, but remained at approximately 3.3 in N-2 fish. The value of b for the three June samples of fish held in sea water was 2.8 whereas in the July sample it was 3.1.

Although a cube relationship of weight on length has been assumed by several investigators, Le Cren (1951) has emphasized that the value of the parameter b usually ranges from 2.5 to 4. Salo and Bayliff (1958) mechanically separated large and small hatchery-reared coho smolts and calculated the weight–length relationships of both groups before planting and after their recovery from downstream traps. The value of b was approximately 3 for large fish at both times and for small fish when released; on recapture the value for small fish was approximately 2.9. The value of b for wild migrating smolts was 2.76. These values are very similar to those reported herein for smolting coho.

Leith and Wyatt (1963) calculated a weight–length relationship from data accumulated throughout two rearing periods in several Oregon State hatcheries. They weighed and measured 2246 young coho ranging in weight from 1 to 37 g and calculated a value for b of 2.986. Unfortunately, they did not report separate weight–length relationships for individual sampling times or hatcheries. Le Brasseur and Parker (1964) calculated the weight–length relationship of pink salmon (*O. gorbuscha*) from shortly after they entered

TABLE I. Parameters and type 2 errors of the least-square fit relationships of fish weight on fork length of various groups of laboratory-reared and wild juvenile coho salmon (log weight, g = log a + b log length, cm).

Date	Sample size (n)	Least-square fit of weight on length ($w = a L^b$)			
		a (mg)	Error	b	Error
N-1 Laboratory reared					
July 20, 1964	40	14.4	2.0	2.82	0.07
Aug. 31, "	68	6.8	1.0	3.25	0.07
Sept. 22, "	57	10.4	1.9	3.08	0.09
Oct. 13, "	124	6.3	0.6	3.31	0.05
Nov. 18, "	91	7.3	1.1	3.24	0.07
Dec. 21, "	126	5.6	0.5	3.34	0.04
N-1A Laboratory reared					
Jan. 12, 1965	73	12.4	2.4	2.97	0.09
Feb. 9, "	56	7.6	2.7	3.18	0.15
Mar. 9, "	55	10.7	2.9	3.02	0.12
Apr. 13, "	55	9.1	2.6	3.08	0.12
May 20, "	55	11.0	3.6	3.00	0.13
June 17, "	42	18.8	8.5	2.81	0.18
N-2 Laboratory reared (tagged)					
Aug. 31, 1964	14	6.2	1.6	3.31	0.12
Sept. 22, "	14	7.4	3.2	3.27	0.20
Oct. 20, "	14	5.0	2.6	3.44	0.23
Nov. 10, "	14	3.9	2.5	3.53	0.28
Dec. 8, "	14	3.4	1.7	3.59	0.22
Jan. 14, 1965	14	4.8	2.8	3.39	0.25
Feb. 9, "	14	4.2	2.3	3.46	0.23
Mar. 9, "	14	5.4	2.6	3.34	0.19
Apr. 15, "	14	5.5	3.0	3.31	0.21
May 20, "	14	10.3	5.2	3.03	0.19
N-3 Laboratory reared					
Jan. 14, 1965	47	5.5	2.1	3.31	0.16
Feb. 9, "	59	17.3	6.5	2.84	0.16
Mar. 9, "	55	11.4	2.9	3.00	0.10
Apr. 13, "	54	7.2	2.9	3.18	0.13
May 20, "	55	10.3	3.0	3.02	0.11
June 17, "	48	6.3	2.2	3.19	0.12
Wild free-swimming fry from Big Qualicum River spawning channel					
Oct. 15, 1965	40	6.2	0.9	3.30	0.07
Wild inactive pre-smolts, Hunt Creek					
Feb. 21, 1966	84	8.8	1.4	3.10	0.08
Wild free-swimming pre-smolts, Hunt Creek					
Apr. 14, 1966	88	13.3	0.9	2.88	0.03

(*Continued*)

TABLE I. Parameters and type 2 errors of the least-square fit relationships of fish weight on fork length of various groups of laboratory-reared and wild juvenile coho salmon (log weight, g = log a + b log length, cm). — (*Concluded*)

Date	Sample size (n)	Least-square fit of weight on length ($w = a\ l.^b$)			
		a (*mg*)	Error	b	Error
Wild pre-smolts entering Qualicum River from Hunt Creek					
Apr. 6, 1965	77	18.6	4.6	2.74	0.12
May 9, 1966	89	10.0	1.5	3.04	0.07
Wild smolts migrating from mouth of Qualicum River					
May 25, 1966	64	9.8	1.6	3.03	0.07
June 2, 1965	45	16.9	5.2	2.84	0.13
Migrating smolts of May 25 held in seawater live boxes					
June 1, 1966	70	14.3	2.7	2.85	0.08
June 13, "	61	17.3	3.7	2.81	0.09
June 27, "	57	17.9	5.3	2.81	0.12
July 20, "	63	9.1	1.8	3.11	0.08

the sea as fry until they were captured as adults. These investigators fitted a linear regression line to the average weights and lengths obtained at each sampling time and determined the slope of this line to be 3.25 which is comparable with the present value of 3.24 (Fig. 3).

The plots of weight on length of individual coho in the smolt and post-smolt stage obtained in the present investigation were similar to those of Houston (1961) for smolt and post-smolt steelhead trout (*Salmo gairdneri*). From observations of the coho plots, together with those of fry, one gains the impression that they consist of a family of curves with a slope of approximately 3.2. If this is correct the intercept, a, of these curves decreases from approximately 7.5 mg in pre-smolt coho to about 5.6 mg during smolting and then increases to about 6.2 mg in post-smolts. The calculated values of b, which were less than 3.2 during smolting, could arise if the fish of any one sample were of various lengths, and if the streamlining was a function of size rather than age, with long fish changing shape earlier than short fish. That this may indeed be so is suggested by the report of Salo and Bayliff (1958). These investigators mechanically separated hatchery-reared coho smolts into two size-groups and found that for a given length small fish were heavier than large fish.

Several other physiological parameters associated with smolting in salmonids have been shown to be mainly, if not wholly, a function of size with age being of minor importance. Thus, Allen (1944) found that there was an apparent relation between size of Atlantic salmon (*Salmo salar*) and the onset of smolt development which causes a salmon to migrate in response to suitable external stimuli, and Elson (1957) showed a relation between size and guanine

deposition. Similarly, salinity tolerance of *S. salar* (Parry, 1958, 1960) and *O. kisutch* (Conte et al., 1966) has been shown to be mainly size-dependent as was the time required for *S. gairdneri* to adapt to sea water (Houston, 1961). In the present investigation, as discussed later, total moisture, solids and nitrogen compositions of juvenile coho were also size dependent.

From the results for pink salmon presented by Le Brasseur and Parker (1964) we have calculated the intercept, a, of the weight–length formula to be approximately 4.3 mg. This value is lower than most of the values for coho presented in Table I but higher than most values for young migrating pink fry obtained by Skud (1955). Salo and Bayliff (1958) used fish lengths in millimeters to derive their weight–length relationships. When these relationships were recalculated[7] for fish lengths in centimeters the intercepts were 11.8 mg for large fish before liberation and 13.1 mg for small fish. On recapture the intercepts were 7.5 mg for large fish, 10.9 for small fish, and 16.4 for wild fish. These values are of the same order of magnitude as those presented in Table I.

Belly Skin Guanine

Guanine levels in belly skin (Fig. 4) appeared to be related to physiological state and lighting conditions rather than to length or weight. Thus, although

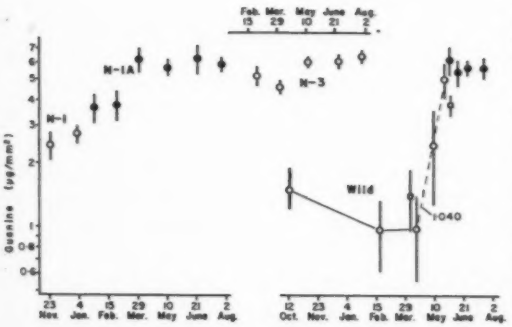

FIG. 4. Changes in belly skin guanine of five groups of juvenile coho salmon. Open circles represent 1964–65 N-1 and N-3 laboratory fish and 1965–66 wild fish in fresh water. Solid circles represent N-1A laboratory fish in fresh water and post migrant wild fish in sea water. The open squares represent 1965 pre-migrant and migrating wild fish in fresh water. The broken line represents the least-square fit of guanine on time of smolting in 1966 wild fish, and the slope of this line is shown on the graph. The vertical bars represent two standard deviations of each sample.

guanine levels in different-sized fish at any one sampling time were similar, there was an increase during early exponential growth as the fish became more streamlined. The fall level in wild fish was 1.6 μg/mm^2 skin. This decreased to 1.0 μg both for fish overwintering among dead leaves and other debris and for fish newly emerged from under the stream banks in April. During expo-

[7] $a = (1000c)\ (10^n)$ where c = intercept and n = slope as determined by Salo and Bayliff (1958).

nential growth in fresh water, guanine levels increased 4% per day to 5 $\mu g/mm^2$ at the time of migration, and remained at approximately 6 $\mu g/mm^2$ during the 2 months in sea water. In laboratory-reared fish, held in light blue tanks with direct lighting, guanine increased from about 3 $\mu g/mm^2$ belly skin in mid-winter to about 6 μg in March and remained at this level for the balance of the experimental period. Johnston and Eales (1967), investigating Atlantic salmon, obtained similar results in that more rapid purine deposition occurred in nature than in the laboratory and that it occurred much later.

Total Lipid

Total lipid was reasonably well related to weight in fish not growing exponentially (Table II). However, during exponential growth, although the general trend of large fish having a higher percentage lipid than small fish (power $d > 1$) was maintained, the relationship between total lipid and weight was poor.

In laboratory-reared N-1 fish total lipid increased with increasing length to approximately 1.3 g/10.5 cm fish (Fig. 5). Similarly in the N-1A fish total lipid increased with increasing length to about 0.9 g/10 cm fish and remained at approximately this value for the remainder of the experimental period. Because of this levelling off in lipid content while both length and weight continued to increase there was a decrease in relative amount of lipid from about 6.5% of body weight in a 10-cm fish to about 3% in a 13-cm fish. In the N-3 fish total lipid per unit length continued to increase to about 1.8 g in a 12-cm fish. There was approximately 0.9 g of lipid in N-3 fish longer than 12 cm.

Unlike laboratory-reared fish total lipid in the wild fish increased from about 1.5% of body weight in the fish sampled in October, February, and April to about 3.5% in migrating smolts and continued to increase to about 4.5% in the fish held in sea water. On a lipid–length basis (Fig. 6) a 10-cm fish contained approximately 0.3 g lipid, and no levelling off or reduction in lipid content per unit length occurred as growth continued. In fact Fig. 6 suggests that total lipid per unit length may have increased in post-migrant fish in sea water, when the total weight per unit length increased as shown in Fig. 3 and 7.

From the results of Lovern (1934) and Hoar (1939) on Atlantic salmon, Kizevetter (1948) on sockeye salmon, and Parker and Vanstone (1966) on pink salmon, the decrease in lipids accompanying the parr–smolt transformation in laboratory-reared coho was expected. The absence of this phenomenon in wild coho cannot be explained and must be the subject of further investigations.

Total Moisture, Solids, and Nitrogen

Total moisture, solids, and nitrogen, which were determined in wild fish only, were linearly related to weight in the size-range studied (1–37 g). However, there was a sharp inflection in each least-square fit line which occurred for moisture and solids at a fish weight of 15 g and for nitrogen at 7.5

TABLE II. Parameters and type 2 errors of the least-square fit relationships of total lipid on fish weight of various groups of laboratory-reared and wild juvenile coho salmon (log lipid, mg = log c + d log weight, g).

Date	Sample size (n)	Least-square fit of lipid on weight ($F = cW^d$)			
		c (mg)	Error	d	Error
N-1 Laboratory reared					
July 20, 1964	20	39.2	6.0	1.34	0.10
Oct, 13, "	10	33.2	17.6	1.32	0.25
Nov, 18, "	9	21.5	5.4	1.51	0.10
Dec. 21, "	10	24.2	5.8	1.48	0.10
Oct. and Nov., 1964	19	25.0	8.1	1.45	0.07
N-1A Laboratory reared					
Jan. 12, 1965	15	15.0	7.0	1.67	0.20
Feb. 9, "	8	56.0	21.6	1.07	0.16
Mar. 9, "	8	25.0	12.9	1.37	0.20
Apr. 13, "	8	20.5	12.7	1.34	0.21
May 20, "	8	1.2	2.0	2.16	0.55
June 17, "	8	7.4	12.8	1.48	0.54
N-3 Laboratory reared					
Feb. 9, 1965	10	16.6	5.9	1.55	0.12
Mar. 9, "	8	26.8	30.6	1.36	0.38
Apr. 13, "	8	12.9	10.8	1.54	0.26
May 20, "	8	2.9	3.9	1.80	0.38
June 17, "	8	8.2	15.0	1.39	0.55
Wild free-swimming fry from Big Qualicum River spawning channel					
Oct. 15, 1965	20	8.4	1.5	1.19	0.16
Wild inactive pre-smolts, Hunt Creek					
Feb. 21, 1966	20	20.1	3.0	1.19	0.15
Wild free-swimming pre-smolts, Hunt Creek					
Apr. 14, 1966	20	9.9	2.2	1.49	0.11
Wild pre-smolts entering Qualicum River from Hunt Creek					
Apr. 6, 1965	26	30.9	8.6	0.80	0.18
May 9, 1966	20	30.3	15.3	1.02	0.22
Wild smolts migrating from mouth of Qualicum River					
May 25, 1966	14	13.7	13.1	1.33	0.33
June 2, 1965	15	3.6	3.5	1.86	0.34
Migrating smolts of May 25 held in seawater live boxes					
June 1, 1966	12	27.3	25.7	1.01	0.36
June 13, "	12	21.8	12.2	1.18	0.18
June 27, "	13	21.2	19.5	1.18	0.30
July 20, "	15	35.3	30.9	1.09	0.26

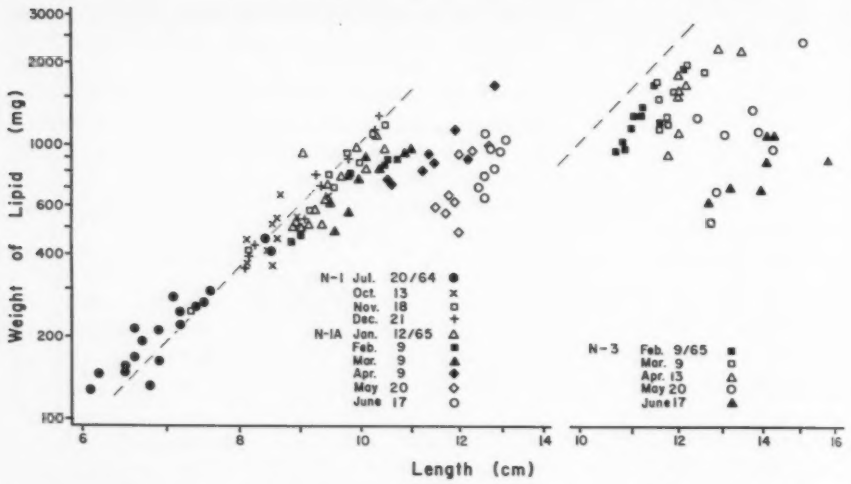

FIG. 5. Total lipid contents of individual laboratory-reared juvenile coho salmon. The broken line on each graph represents the calculated least-square fit line of total lipid on length of the October and November N-1 samples: log lipid, mg = log 0.0173 + 4.7676 log length, cm (total lipid = c (weight)^d = ca^d (length)^{bd}; a = 1/215 [(124 × 6.3) + (91 × 7.3)] = 6.723; b = 1/215 [(124 × 3.31) + (91 × 3.24)] = 3.28; ca^d = 24.958 (6.723)$^{1.4635}$ = 0.0173; bd = 3.28 × 1.4535 = 4.7676.

g (Table III). The shift in moisture–solids composition occurred regardless of whether the fish were in fresh or salt water. Thus, some of the pre-migrant May 9 and migrating May 25 fish in fresh water weighed more than 15 g, whereas some fish in sea water, including one fish of July 20, weighed less. The shift in total nitrogen composition occurred in fresh water and was also a function of weight rather than physiological state since fish of less than 7.5 g were present in all samples up to and including migrating smolts. All fish in sea water weighed more than 7.5 g. If these relationships are valid for fish larger than 37 g then moisture, solids, and nitrogen would approach limiting values of 72, 28, and 3.1% respectively of body weight. These limiting values are comparable with the values of 70, 30, and 3.3% for moisture, solids, and nitrogen found in prespawning adult sockeye by Kizevetter (1948).

During exponential growth, in both fresh and sea water, growth in weight was accompanied by increased moisture, solids, and total nitrogen (Fig. 2 and 7). However, moisture did not increase as rapidly as weight, whereas solids and nitrogen increased more rapidly. During this growth period in fresh water total weight increased 4.4% per day whereas moisture increased 4.3% per day, solids 4.7% per day, and nitrogen 4.9% per day. In sea water the decreased growth rate in weight of 1.6% per day was accompanied by daily increases of 1.5, 2.0, and 1.8% in moisture, solids, and nitrogen respectively.

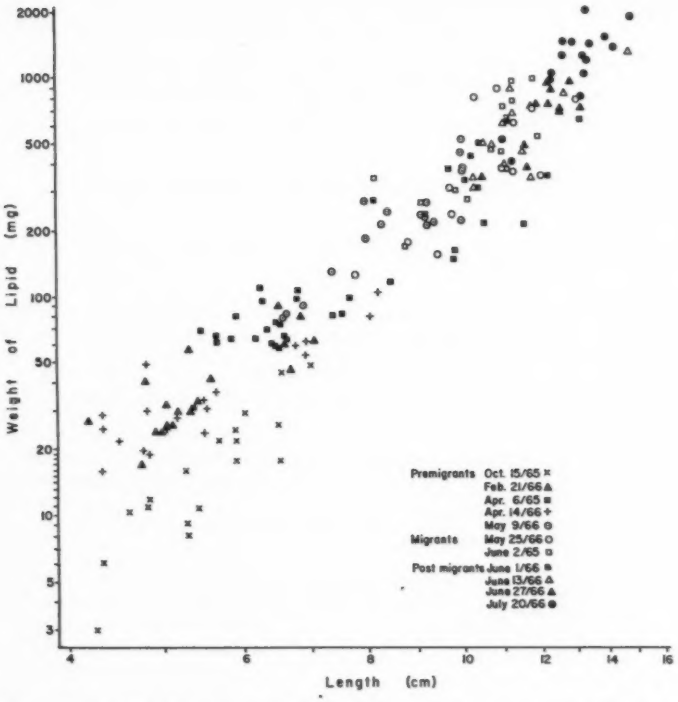

FIG. 6. Total lipid contents of individual pre-migrant and migrating wild coho in fresh water and post-migrant wild coho confined to boxes in sea water.

TABLE III. Parameters and type 2 errors of the least-square fit relationships of total moisture, solids, and nitrogen on weight of wild juvenile coho salmon sampled between October 15, 1965, and July 20, 1966. (Y, mg = $e + f$ weight, g).

	Fish weight (g)	Sample size	e	Error	f	Error
Moisture	<15	90	78	15	790	2
	>15	38	1150	147	720	6
Solids	<15	90	−78	15	210	2
	>15	38	−1150	147	280	6
Nitrogen	<7.5	50	−1.9	1.1	22.5	0.3
	>7.5	76	−61.1	5.1	31.0	0.3

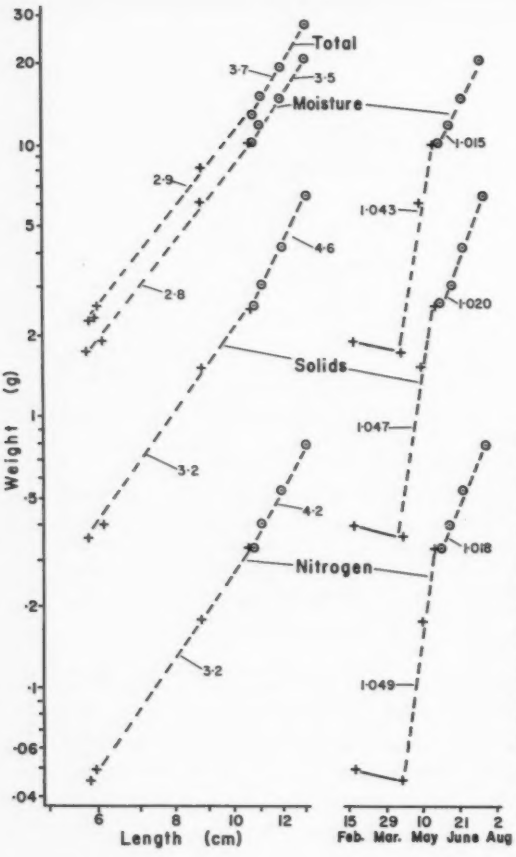

FIG. 7. Fitted weights of total moisture, solids, and nitrogen in 1965–66 wild coho of the mean weight at each sampling time. The weights of these components are plotted against mean lengths and sampling dates. The mean weight of fish at each sampling time is plotted against mean length here and in Fig 3 and against sampling date in Fig. 2. The crosses represent pre-migrants and migrating fish in fresh water; the circles, post-migrant fish confined to boxes in sea water; broken lines least-square fit line of components on length or time, the slopes of these lines being shown on the graphs.

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Principal Fatty Acids of Depot Fat and Milk Lipids from Harp Seal (*Pagophilus groenlandica*) and Hooded Seal (*Cystophora cristata*)[1,2]

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ABSTRACT

The fatty acid compositions of six samples of depot fat taken from harp seals (*Pagophilus groenlandica*), ranging in age from 1 to 2 days to adult, and a sample of milk lipids, were determined by gas–liquid chromatography (GLC). Three depot fat samples taken from hooded seals (*Cystophora cristata*), a sample of milk lipids from this species, and commercial seal oils from 4 years' production were similarly analyzed.

No significant differences could be found between the composition of the milk lipids and the depot fat of the harp seals at the different ages, other than slightly lower iodine values in the younger animals (avg 140.6 vs. 148.9). The lipid samples from hooded seals had low iodine values (107–127) and correspondingly lower concentration of highly unsaturated fatty acids. The ratio of the fatty acids 22:5ω3/22:6ω3 could be used to differentiate between depot fat from harp seals (ratio 0.51–0.74) and that from hooded seals (ratio 0.25–0.42) in the samples analyzed.

Commercial oils, which consist essentially of oil from harp seals, were similar in composition to oil prepared from this species alone.

No difference could be found in the iodine values or fatty acid compositions of samples taken from various parts of the animal or from samples representing a cross section of blubber.

INTRODUCTION

The harp seal (Greenland seal, saddle seal) *Pagophilus groenlandica*, the most abundant of the seals occurring in the North Atlantic and arctic regions, is of considerable economic importance. In their breeding areas in the Gulf of St. Lawrence and off Newfoundland and Labrador as many as 295,000 animals have been harvested in a single year (Mansfield, 1967).

The hooded seal *Cystophora cristata* also breeds on the ice in the same areas, but occurs in much smaller numbers; the catch ranges between 100 and 14,000 animals per year with an average of 5800 for 1949–58. Much larger herds can be found in the area southwest of Spitsbergen where an average of 70,000 are taken each year.

The only quantitative data available on the lipids of the harp and the hooded seals are based on the analysis of a commercial seal oil sample from Newfoundland which was most likely prepared from a mixture of blubber from these two species (Burke and Jasperson, 1944). The harvest of harp

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seals is much greater than of hooded seals in this area; consequently, commercial oils are essentially harp blubber oils.

A qualitative study by gas–liquid chromatography (GLC) of the fatty acids of commercial seal oil was published (Ackman et al., 1963). Quantitative GLC analyses of the fatty acid composition of the following lipid materials taken from other seal species have been reported: blubber fat from the common or harbor seal *Phoca vitulina* (Jangaard et al., 1963); blubber fat and milk lipids from grey seal *Halichoerus grypus* (Ackman and Burgher, 1963; Ackman and Jangaard, 1965); and the fatty acid composition of lipids from southern elephant seal *Mirounga leonina* (Tsuyuki and Itoh, 1966). Hilditch and Williams (1964) list several analyses of lipids from other species of seals carried out by distillation or crystallization procedures. Incomplete analysis of the fatty acids of milk from northern fur seal (*Callorhinus ursinus*) and Weddell seal (*Leptonychotes weddelli*) have been published (Ashworth et al., 1966; Glass et al., 1967). The object of this study was to make certain that the data on seal lipids included accurate and reliable analyses of the fatty acid composition of blubber and the milk lipids from both harp and hooded seals. Samples of commercial seal oil from several years' production were analyzed also for comparative purposes.

EXPERIMENTAL

The commercial seal oils and most of the blubber samples were obtained from Blandford, N.S., through the courtesy of Karl Karlsen and Co. Ltd., Halifax, N.S. The blubber samples were kept frozen until rendered, and any discolored or oxidized material on the surface was then trimmed off. It was shown by iodine value (I.V.) and GLC analysis that the composition of a cross section of blubber was uniform. The milk and blubber samples from lactating hooded and harp females and their pups were collected in the Gulf of St. Lawrence by Dr D. E. Sergeant of the Arctic Biological Station, Fisheries Research Board of Canada, Ste. Anne de Bellevue, Que.

The blubber fat of young seals contains very little connective tissue; consequently, the oil was rendered by macerating the blubber in a Waring Blendor. These and subsequent operations were carried out under a blanket of nitrogen or carbon dioxide. Anhydrous sodium sulfate and a small amount of filter aid was added and after filtration the oil obtained was colorless. The samples of blubber collected in 1968 were extracted with chloroform and lipids were extracted from the milk samples by the method of Bligh and Dyer (1959). The fat content of the harp seal milk was 42.9%, of the hooded seal 23%.

After saponification and removal of the unsaponifiable fraction, the fatty acids were esterified with boron trifluoride–methanol.

GLC of the methyl esters was carried out on a Barber Coleman Model 10 equipped with a Model 5121 flame ionization detector. The glass columns (3 mm inside diam, 6 ft long) were packed, respectively, with 11% EGSS-X and 12% EGSS-Y on 100–120 mesh Gas-Chrom P (Applied Science Laboratories, Inc., State College, Pa.). Tentative identification of the peaks was

made by log plot and separation factor procedures (Ackman and Burgher, 1965) and correction factors (Ackman and Sipos, 1964) for quantitative determinations were applied. Several other analyses were carried out on a Perkin Elmer 229 with a BDS capillary column (150 ft long).

The analyses of hooded seal depot fat samples from the Spitsbergen–Jan Mayen area were made by the senior author at the Norwegian Fisheries Research Laboratory, Bergen, in 1951.

RESULTS AND DISCUSSION

The properties and fatty acid compositions of depot fats and milk lipids from harp and hooded seals and of four samples of commercial seal oils are tabulated in Tables I and II.

Harp Seal

From Table I it can be seen that the average I.V. shows some increase with age, 140.6–148.9, but the number of samples analyzed (12) were too few to make this a conclusive statement. The newborn pup (1 day) had a very thin layer of blubber and it was difficult to obtain a sample free of meat for extraction. The exceptionally low I.V. of this oil was not included in the averages.

Approximately 97% of the Canadian commercial seal oil is prepared from harp seal blubber. Thus the fatty acid compositions of these oils are similar to the composition of the blubber fats of the individual harp seals, and the average I.V. (148.3) is very close to the average for individual adult harp seals (148.9).

Ackman et al. (1965) found that the composition of the blubber of fin whale varied with the different cross-sectional areas sampled. Therefore, we divided a sample of blubber from an adult female harp seal into an outer, middle, and inner fraction and rendered them separately to make a similar determination for this seal. I.V.'s and GLC analysis failed to reveal any differences in fatty acid composition between the three sections, and the I.V. in Table I and the analysis given in Table II represent an average of all three.

The data in Table II indicate that there are no significant differences between the fatty acid composition of milk lipids and that of the blubber samples taken at various ages. The pups grow very rapidly in the 3–4 week nursing period (from approximately 15 to 80 lbs) and a large percentage of the weight gain is due to the deposit of fat in the blubber. The thickness of this fat layer increases from approximately 3 to 40 mm in this period. The fat content of the milk sample analyzed was high (42.9%) and it appears from the fatty acid analyses that most of this fat was deposited directly in the blubber of the pups.

Ackman et al. (1968) had found an enrichment in hexadecanoic acid (16:0) in the fatty acids of the lipids from grey seal and fin whale milk as compared with the depot fats but this trend was not noted in the milk lipids

TABLE I. Properties of seal blubber samples and commercial oils.

Harp seal depot fat

Approximate age (*days*)	Year collected	Thickness of blubber (*mm*)	Iodine value, Wijs	
1	1962	3	(110.7)	
1–2	1963	3–7	141.4	
4–5	1962	8	133.7	
5–6	1963	12–15	132.7	Avg I.V. 140.6
10	1963	ca. 30	154.4	
14	1963	38–40	142.8	
21	1962	26	138.9	
2 years	1963	35	159.1	
2 years	1962	33	146.6	
Female >4 years	1963	40–50	157.5	Avg I.V. 148.9
Female ≈4 years	1962	36	137.1	
Male >4 years	1963	40–45	144.2	

Commercial oils

Year produced	Iodine value, Wijs	Saponification value	Unsaponifiable matter
1949	149.5	189.6	0.23
1953	146.6	193.7	0.35
1954	155.6	195.6	0.40
1955	146.0	188.5	0.21
1960	149.7	193.3	0.32
1961	146.0	192.6	0.18
1962	148.5	189.3	0.24
1964	144.9	191.3	0.31
Avg	148.3	191.7	0.28

Hooded seal depot fat

Approximate age	Year collected	Thickness of blubber (*mm*)	Iodine value	Saponification value	Unsaponifiable matter
2–3 days	1968 Gulf	–	115.9	–	–
5–6 days	1962 Nfld.	15–20	127.2	–	–
Female, adult	1968 Gulf	–	107.1	–	–
2 samples	1949–50				
<2 weeks	Spitsbergen	–	142.7–148.2 Avg = 145.5	187.9–188.1 Avg = 188.0	0.2, 0.2
4 samples	1949–50				
<2 weeks	Greenland–Labrador	–	137.6–140.0 Avg = 138.7	186.3–189.6 Avg = 188.7	0.2, 0.4 0.2, 0.2

TABLE II. Fatty acid compositions of depot and milk lipids from harp seal, hooded seal, and commercial seal oils (weight %).

	Harp seal, depot fat							Hooded seal, depot fat				Commercial oils							
	Approximate age							Approximate age				Year produced							
Fatty acid	1–2 days	5–6 days	14 days	2 years	Female >4 years	Male >4 years	Milk lipids	2–3 days	5–6 days	Adult female	Milk lipids	1954	1961	1962	1964	Avg	Depot fat, harbor seal[a]	Depot fat, grey seal[b]	Milk lipids, grey seal[c]
14:0	4.15[e]	4.50	3.53	3.97	4.42	4.06	4.33	3.89	6.05	3.24	3.62	4.14	4.78	4.27	4.35	4.4	3.3	4.08	3.23
14:1ω5[d]	1.04	0.65	0.75	0.90	1.09	1.17	0.61	0.70	0.86	0.74	0.70	0.93	1.24	0.84	0.72	0.9	1.1	1.83	0.29
15:0	0.30	0.41	0.19	0.28	0.36	0.23	0.32	0.26	0.35	0.25	0.54	0.34	0.29	0.34	0.29	0.3	0.07	0.30	0.19
16:0	10.19	9.20	8.89	9.63	7.87	6.75	9.02	11.95	10.41	7.14	9.48	7.37	7.92	8.72	8.95	8.2	6.5	7.69	17.91
16:1ω7[d]	19.44	16.88	18.28	14.51	17.10	14.97	17.03	16.43	10.54	13.14	13.54	17.90	16.83	17.79	19.30	18.0	17.6	14.88	15.86
16:2ω4	0.44	0.53	0.20	0.63	0.59	0.36	0.46	0.36	0.23	0.50	0.37	0.31	0.34	0.47	0.33	0.4	0.5	0.60	0.11
16:3ω4	0.15	0.37	0.26	0.27	0.49	0.31	0.12	0.20	0.21	0.44	0.24	0.29	0.24	0.33	0.22	0.3	0.1	0.36	0.05
16:4ω1	0.16	0.21	0.39	0.25	0.33	0.41	0.20	0.26	0.42	0.15	0.15	0.18	0.26	0.15	0.16	0.2	0.2	0.18	0.06
17:0	0.34	0.41	0.51	0.35	0.43	0.43	0.36	0.42	0.51	0.55	0.46	0.40	0.45	0.30	0.46	0.4	0.1	0.10	0.30
17:1ω8[d]	0.17	0.21	0.19	0.20	0.24	0.22	0.10	0.17	0.10	0.17	0.29	0.35	0.27	0.19	0.11	0.2	0.2	0.36	0.26
18:0	1.93	2.04	1.36	1.81	1.19	1.27	1.20	1.97	1.55	1.22	2.81	0.90	1.13	1.05	1.04	1.0	0.4	1.00	1.77
18:1ω9[d]	25.37	23.69	23.83	25.60	21.78	24.01	20.83	31.16	24.60	31.08	27.18	24.47	23.25	24.88	26.05	24.7	30.2	24.46	30.61
18:2ω6	0.84	1.17	0.71	1.10	1.89	0.89	1.39	1.53	1.86	2.51	1.34	1.44	1.40	1.42	1.26	1.4	0.8	1.59	0.57
18:3ω3	0.19	0.37	0.31	0.45	0.23	0.47	0.24	0.39	0.97	0.34	0.58	0.48	0.44	0.20	0.40	0.4	0.2	0.66	0.40
18:4ω3	0.73	0.83	0.75	1.41	0.88	0.64	1.16	0.85	2.62	0.83	1.13	1.51	1.31	1.18	0.93	1.2	0.7	1.44	1.06
19:1ω8[d]	0.10	0.15	0.12	0.16	0.12	0.12	0.20	0.10	0.13	0.10	0.17	0.15	0.18	0.19	0.14	0.2	0.1	0.04	0.06
20:1ω9[d]	12.22	12.28	15.53	10.20	13.49	16.84	13.90	11.82	17.84	20.21	15.00	12.60	14.59	12.46	10.44	12.5	13.6	8.92	2.74
20:2ω6	0.19	0.22	0.19	0.15	0.23	0.19	0.22	0.26	0.18	0.47	0.23	0.34	0.20	0.21	0.29	0.3	T	0.19	0.04
20:4ω6	0.54	0.49	0.47	0.38	0.35	0.35	0.54	0.39	0.23	0.17	0.74	0.62	0.33	0.56	0.57	0.5	0.3	0.50	1.42
20:4ω3	0.41	0.65	0.40	0.47	0.43	0.33	0.60	0.31	0.82	0.23	0.81	0.53	0.29	0.57	0.61	0.5	0.2	0.67	0.38
20:5ω3	5.61	4.91	6.30	8.16	7.91	5.99	9.03	5.46	4.00	2.61	6.81	7.50	6.36	7.32	8.62	7.5	5.5	5.71	8.82

(*Continued*)

TABLE II. Fatty acid compositions of depot and milk lipids from harp seal, hooded seal, and commercial seal oils (weight %). — (*Concluded*)

Fatty acid	Harp seal, depot fat							Hooded seal, depot fat				Commercial oils							
	Approximate age							Approximate age				Year produced							
	1–2 days	5–6 days	14 days	2 years	Female >4 years	Male >4 years	Milk lipids	2–3 days	5–6 days	Adult female	Milk lipids	1954	1961	1962	1964	Avg	Depot fat, harbor seal[a]	Depot fat, grey seal[b]	Milk lipids, grey seal[c]
21:5ω2?	0.15	0.27	0.22	0.28	0.34	0.23	0.36	0.20	0.34	0.13	0.23	0.38	0.22	0.25	0.32	0.3	0.3	0.47	0.36
22:1ω11[d]	2.30	2.86	4.12	3.86	4.42	7.10	5.21	3.80	5.75	7.26	5.03	4.54	5.00	3.45	2.96	4.0	6.0	1.59	0.50
22:5ω3	3.91	5.19	3.71	4.30	5.05	3.67	3.39	1.33	1.52	1.21	1.65	3.83	4.24	4.53	3.58	3.9	4.2	5.70	3.50
22:6ω3	6.94	8.85	6.89	8.41	6.86	6.87	6.49	3.61	6.03	3.47	3.91	6.58	7.06	6.92	6.20	6.7	7.5	15.41	8.14
24:1ω9[d]	0.24	0.25	0.31	0.28	0.24	0.27	0.21	0.19	0.27	0.38	0.40	0.30	0.33	0.21	0.16	0.3	0.1	0.10	
Others	1.95	2.41	1.58	1.99	1.67	1.85	2.48	1.99	1.61	1.47	2.59	1.72	1.05	1.70	1.54	1.30			
Ratio $\frac{16:0}{16:1}$	0.52	0.55	0.49	0.66	0.46	0.45	0.53	0.73	0.99	0.54	0.70	0.41	0.47	0.49	0.46	0.46	0.37	0.52	1.13
$\frac{22:5}{22:6}$	0.56	0.59	0.54	0.51	0.74	0.53	0.52	0.37	0.25	0.35	0.42	0.55	0.57	0.55	0.54	0.55	0.56	0.37	0.43
Calc. I.V.	130.3	137.9	133.4	148.2	145.4	133.8	140.3	110.1	121.0	104.6	118.9	142.3	138.4	140.6	140.8	140.9			
Wijs I.V.	141.4	132.7	142.8	159.1	157.5	144.2	–	115.9	127.1	107.1	–	155.6	146.0	148.5	144.9	148.7	142.0	177	154

[a]Jangaard et al., 1963.
[b]Ackman and Jangaard, 1965.
[c]Ackman and Burgher, 1963.
[d]Several isomers may be present.
[e]Data are given to two places of decimals for comparative purposes only.

from harp or hooded seals. The findings by Cama and Meara (1953) that seal milk fat has a lower I.V. than seal blubber could not be confirmed either.

The saturated fatty acids from a sample of blubber oil from an adult, female harp seal was recently analyzed separately by urea complex treatment and GLC on open-tubular columns (Ackman and Hooper, 1968). A number of branched chain acids were quantitatively determined, the multibranched chain acids pristanic, phytanic and 4,8,12-TMTD being found among others.

Hooded Seal

The three samples of depot fat from hooded seals analyzed show some differences from the harp seal lipids. The I.V.'s are considerably lower, especially the samples from the adult female and the pup obtained in March 1968 (107–116). This is obviously not a characteristic of the species, since a number of samples from the Spitsbergen herd (Table I) had I.V.'s similar to those found in harp seals in this study (138–149). Mansfield (1967) points out that the hooded seal feeds, among other fish species, on deepwater fish such as Greenland halibut. Since Greenland halibut has been shown to have a very low I.V. oil (92–99) and a very high oil content (15–20%) (Ackman et al., 1967), heavy feeding on this fish could conceivably affect the depot fat composition. If this is so, the milk lipids and subsequently the depot fat of the pup would similarly be affected.

The most characteristic difference between hooded seal and harp seal depot fats is the lower content of 22:5ω3 fatty acid in the lipids of the hooded seal. The ratio of the fatty acids 22:5ω3/22:6ω3 is in the range of 0.25–0.42 for this species (and the grey seal) and 0.52–0.74 for the harp seal, harbor seal, and commercial seal oil.

The fatty acid composition of the milk lipids is very similar to that of the depot fat, and no enrichment of any specific fatty acids could be found.

To demonstrate that the composition is uniform throughout the blubber, samples were taken of the depot fat of a 5–6-day-old pup ("blueback") from the neck, belly, back, and tail. No significant differences in I.V.'s or fatty acid composition could be found, and the values given in Tables I and II for this animal are the averages of these four samples.

The overall pattern of fatty acid composition in these two seals is broadly similar to earlier analyses of marine mammals reported from this laboratory, i.e. harbor seal, grey seal, and fin whale. The most characteristic difference in composition from fish oils of similar I.V., for instance cod liver oil (Jangaard et al., 1967), is the large amounts of 16:1 fatty acid relative to the 16:0 fatty acid found in seal oils. The 22:5ω3 fatty acid is also usually present in larger quantities relative to the 22:6ω3 fatty acid.

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Karl Karlsen and Co. Ltd., Halifax, N.S. kindly donated the other blubber and commercial oil samples. Mrs C. A. Eaton provided additional technical assistance.

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Recent Trends in Subsurface Temperatures in the Gulf of Maine and Contiguous Waters[1]

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ABSTRACT

A comparison was made of 1955–60 and 1961–66 monthly mean 200-m temperatures in eight 1-degree quadrangle areas in the Gulf of Maine and along the Continental Slope between Nova Scotia and Long Island. Temperatures were appreciably lower in all areas during the latter period. The subsurface temperature trends paralleled trends in surface temperatures previously documented. The distribution of temperature at 200 m along the edge of the Continental Shelf during March, May–June, and September 1965 and 1966 and the distribution of temperature, salinity, and dissolved oxygen on sections made across the Continental Shelf in September 1954, 1965, and 1966 showed that the cooling and warming trends are accompanied by changes in the composition of the subsurface water. Cold years occur when Slope Water is displaced or modified by Coastal Water of Labrador origin. Warm years occur when Slope Water borders upon the 200-m isobath and the ratio of Coastal to Central Atlantic Water is low.

INTRODUCTION

Clear evidence exists of an alternation in sea surface temperatures along the coast of New England and the Maritime Provinces (Taylor et al., 1957; Lauzier, 1965; Stearns, 1965). A warming trend began in the early 1940's and reached a maximum during 1952–53. This rise in temperature has been followed by a cooling trend which has continued with only minor interruptions through 1967. Although less well-documented, similar warming and cooling trends have occurred offshore and within water masses (Taylor et al., 1957; Lauzier, 1965, 1967; Colton, 1968). Most of the published offshore observations have been confined to the Continental Shelf and to depths of 100 m or less. In this paper an analysis is made of the available subsurface temperature data in the Gulf of Maine and along the edge of the Continental Shelf from Nova Scotia to Long Island to determine if the trends observed in the surface layers are reflected in the deeper strata.

The subsurface layer, the upper depth limit of which is usually between 150 and 200 m, is relatively isolated from seasonal factors such as wind stirring and solar heating. Unlike the surface layer, which is characterized by pronounced seasonal variations and a complex and unstable temperature and salinity structure, the structure of the subsurface layer is relatively stable and governed by the waters adjacent to it.

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Our interest in subsurface temperature trends stems from the fact that if these trends parallel those in the surface layers, the faunal communities in the deeper waters of the Gulf of Maine and the Continental Slope are subject to long-term temperature variations similar to those experienced by the fauna in relatively shoal areas of the Continental Shelf. Furthermore, since the temperature–salinity characteristics of subsurface water masses can be used to define their component water types, it should be possible to determine the sources of the subsurface water during periods of warming and cooling and thus the direct cause of the temperature change.

THE DATA

A tabulation of temperature data from the file of bathythermograph and oceanographic station observations at the Woods Hole Oceanographic Institution revealed that during the warming period of 1945–53 the number of observations was insufficient to determine valid average subsurface temperatures for any location within the area of concern. Since 1955 the data appear to be adequate to determine monthly subsurface temperatures if several year's observations within 1-degree quadrangles are averaged. Monthly mean 200-m temperatures were determined for the periods 1955–60 and 1961–66 within the eight 1-degree quadrangle areas shown in Fig. 1. Areas I–III are over the three deep basins of the Gulf of Maine, area IV is at the mouth of the Northeast Channel which separates Georges and Browns banks, and areas V–VIII are along the Continental slope. Observations were relatively few for any month within a given year in any quadrangle and these observations were generally weighted in favor of certain days (dates). To offset possible

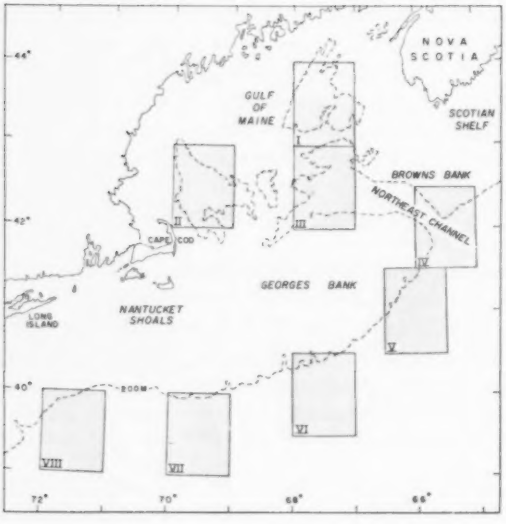

FIG. 1. The location of the eight 1-degree quadrangle areas.

bias in determining monthly means, all data for a given day were averaged and the 6-year monthly means based on the daily means rather than on the total number of observations.

The 6-year monthly mean temperatures at 200 m in the eight areas are plotted in Fig. 2 and 3. The months and years in which temperature data were

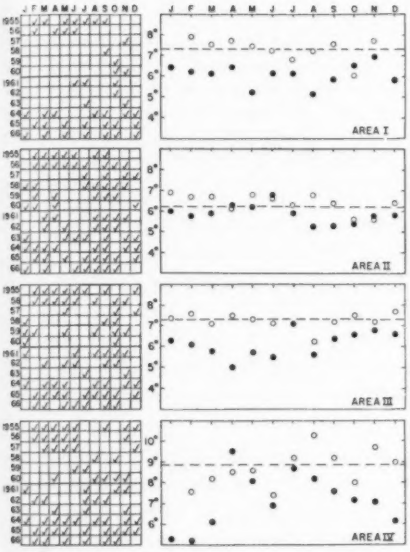

FIG. 2. Monthly and annual mean temperatures at 200 m, areas I–IV. The 1955–60 monthly means are shown by open circles, the 1961–66 monthly means by solid circles. The long-term annual means are indicated by a broken line. Check marks indicate the months and years in which observations were made.

obtained are indicated by check marks. The long-term annual mean 200-m temperatures are shown by a broken line. These long-term values are from Schroeder (1963) and are based on 1-degree quadrangle averages of all available temperatures in the Woods Hole Oceanographic Institution data collection until the end of 1962. For areas IV, V, and VI which do not coincide with the whole-degree latitude–longitude quadrangles used by Schroeder, long-term 200-m temperature values from overlapping whole-degree quadrangles were averaged.

With only a few exceptions (April: areas II and IV; June: area II; July: area III; September: area V; October: areas I and V; and November: area II) the 1960–66 monthly mean 200-m temperatures were lower than the corresponding monthly mean temperatures for 1955–60. Six of these eight anomalies were in months which included 1963 observations. In this year there was a temporary interruption in the downward trend of sea surface temperatures both inshore at Boothbay Harbor, Maine (Welch, 1967), and offshore over the Grand Banks and Georges Bank (Lee et al., 1967). In addition the data of Schopf (1967, Fig. 2) show that bottom temperatures on the Scotian Shelf, Georges Bank, Nantucket Shoals, and in the Gulf of Maine were appreciably warmer in July, August, and December 1963 than in these months during 1964 and 1965.

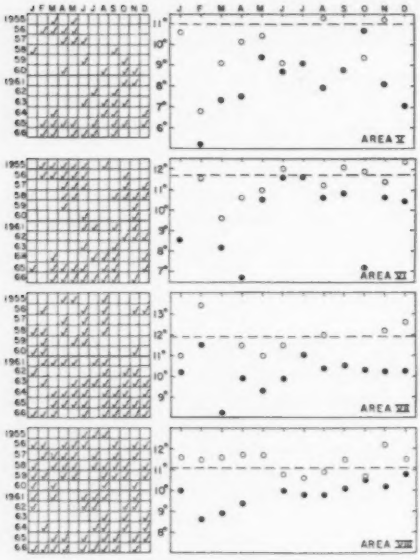

FIG. 3. Monthly and annual mean temperatures at 200 m, areas V–VIII. The 1955–60 monthly means are shown by open circles, the 1961–66 monthly means by solid circles. The long-term annual means are indicated by a broken line. Check marks indicate the months and years in which observations were made.

No consistent seasonal trend existed in the 200-m monthly mean temperatures or in the magnitude of the monthly mean temperature differences for the two time periods in any of the areas. The monthly temperature variation and the magnitude of the monthly temperature differences in the two time periods were least in area II and tended to be greater along the Continental Slope than within the Gulf of Maine. With the exception of area V, yearly mean temperatures based on 1955–60 data closely paralleled Schroeder's long-term means. In area V, the 1955–60 yearly mean was appreciably lower (2.3 degrees C) than the long-term mean. With the exception of area II, the 1960–66 yearly mean temperatures were well below Schroeder's long-term means. In area II, the 1961–66 yearly mean was only slightly lower (0.3 degrees C) than the long-term mean.

Seasonal surface-température curves based on monthly mean temperatures at Boothbay Harbor, Maine, for 1955–60 and 1961–66 (Fig. 4) show temperature trends similar to those in the subsurface waters. In most months and areas, however, the difference in the mean 200-m temperatures for the two 6-year periods was greater than the difference in mean surface temperatures at Boothbay Harbor. Only in area II was the yearly mean difference between the two time periods less at 200 m (0.6 degrees C) than at Boothbay Harbor (0.9 degrees C).

In Fig. 5 the distribution of temperature at 200 m along the edge of the Continental Shelf and in the Northeast Channel during March, May–June, and September 1965 and 1966 is compared with the long-term annual mean and minimum 200-m values in this area. The 1965 and 1966 temperature

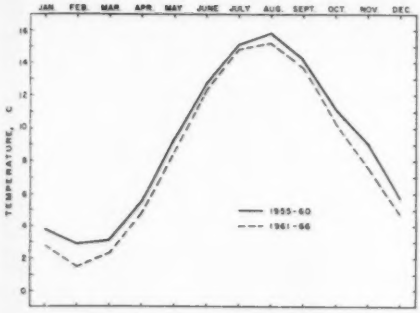

FIG. 4. 1955–60 and 1961–66 mean seasonal temperatures, Boothbay Harbor, Maine.

distributions are based on in situ bathythermograph observations obtained during quarterly environmental surveys conducted by the U.S. Bureau of Commercial Fisheries (Colton et al., 1968). The long-term distributions are based on the average and the minimum temperatures for 1-degree quadrangles given by Schroeder (1963). In both 1965 and 1966 the monthly temperatures adjacent to the 200-m isobath were lower than the long-term mean. In most cases the 1965 and 1966 monthly temperatures were higher than the long-term minimum temperatures. In March 1966, however, the 200-m temperatures were lower than the long-term minimum temperatures in sections adjacent to the 200-m isobath off southern New England, the southeast part of Georges Bank, and the Scotian Shelf.

If we consider the contour of the 9 C isotherm at 200 m to be the northern limit of Slope Water (Worthington, 1964), the long-term annual mean temperature distribution at 200 m would indicate that, in general, Slope Water borders upon the 200-m isobath from Cape Hatteras east to approximately 64°00′W. The distribution of temperature at 200 m during 1965 and 1966 indicates that in these years the northern boundary of the Slope Water was considerably south of its average position. Worthington (1964) concluded that any water colder than 9 C at 200 m could be traced to the Labrador Basin. It would appear that the southerly shift in the normal position of the Slope Water in 1965 and 1966 was due to an abnormal influx of Coastal Water of Labrador origin.

The available salinity data are not sufficient to establish subsurface salinity norms for the area as a whole or to compare the 1955–60 and 1961–66 mean salinity characteristics of the subsurface water in any of the eight 1-degree quadrangle areas on either a monthly or yearly basis. A few oceanographic section data are suitable, however, for a comparison of the inshore and offshore distribution of chemical and physical properties at the end of the warming trend and during the current cooling trend. In Fig. 6 the distribution of temperature, salinity, and dissolved oxygen on sections made along meridian 65°30′W by the *Albatross IV* in September 1965 and 1966 is compared with the distribution of these properties on a section made along meridian 65°00′W by the *Atlantis* in September 1954.

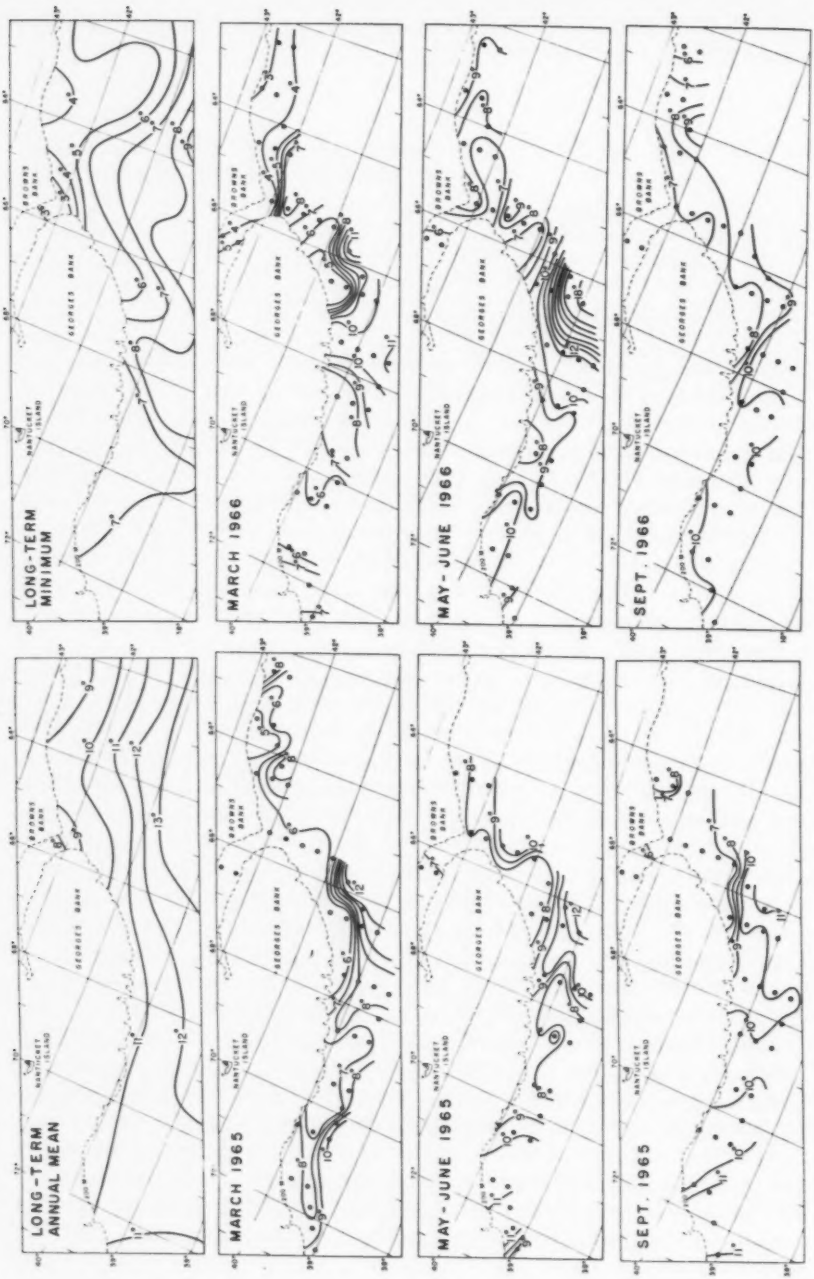

FIG. 5. Comparison of the temperature distribution at 200 m during March, May–June, and September 1965 and 1966 with long-term annual mean and minimum distributions.

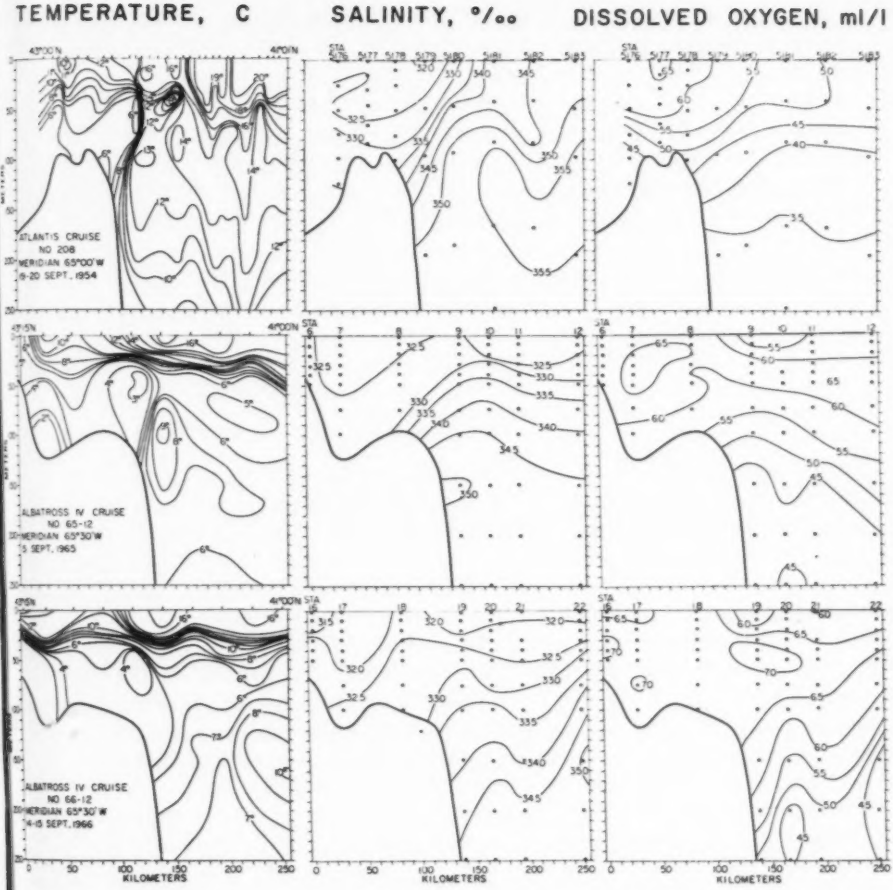

FIG. 6. Temperature, salinity, and dissolved oxygen profiles, September 1954, 1965, and 1966.

Subsurface temperatures and salinities were appreciably higher in 1954 than in 1965 and 1966. At the southern-most stations, the 1954 temperature and salinity values were higher in the surface layer as well. If we consider a temperature of 9 C and a salinity of 35‰ at 200 m as roughly defining the northern limit of Slope Water, the Slope Water boundary coincided with the 200-m isobath in 1954, but was south of 41°00′N lat in 1965 and 1966. Dissolved oxygen values at corresponding depths were appreciably higher in 1965 and 1966 than in 1954. The dissolved oxygen concentrations at depths of 100, 150, and 200 m south of the Continental Shelf corresponded closely to those typical of Slope Water in 1954 and to those typical of Coastal Water in 1965 and 1966 (McLellan, 1957, Table II).

FIG. 5. Comparison of the temperature ... mean and minimum distributions

Temperature–salinity data at 150, 200, and 250 m for the five most southerly *Atlantis* stations in September 1954 and for the four most southerly *Albatross IV* stations in September 1965 and 1966 are plotted in Fig. 7. The *Albatross IV* data are based on observed values at these depths whereas the *Atlantis* data are based on interpolated values. The temperature–salinity curves for Central Atlantic Water, Slope Water, and Coastal Water are also shown. The approximate depths in meters at which waters of various temperature–salinity characteristics are found are indicated by numbers adjacent

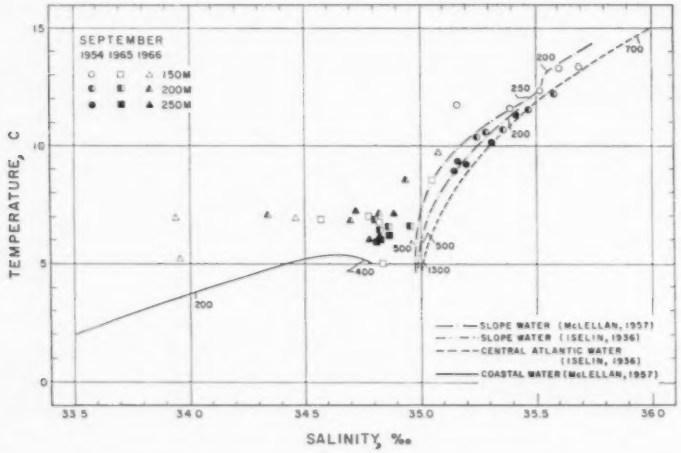

FIG. 7. Temperature–salinity relations at *Atlantis* stations 5179–5183, September 1954 and *Albatross IV* stations 9–12 and 19–22, September 1965 and 1966.

to the curves. The Central Atlantic Water curve is from Iselin (1936) and is based on observations made in the western Sargasso Sea. The Slope Water curve of Iselin (1936) is for waters off Chesapeake Bay. The Slope Water curve of McLellan (1957) is for waters off the Scotian Shelf. The Coastal Water curve (McLellan, 1957) is based on observations made in the Cabot Strait. In describing this water Worthington (1964) used the term "Labrador-Coastal" instead of "Coastal" to indicate that this water is formed by a mixture of Labrador and Slope Water in the region immediately west of the Grand Banks and to distinguish this subsurface water from the surface water over the Continental Shelf. An excellent summary of the temperature–salinity characteristics, composition, and origin of these water masses is given by McLellan (1957).

The temperature–salinity relations confirm the conclusions drawn from the section data. The subsurface water bordering the Continental Shelf south of Browns Bank in September 1954 was Slope Water and that in September

1965 and 1966 was Coastal Water. The temperature–salinity characteristics of the Slope Water in 1954 coincide more closely with the Slope Water curve of Iselin (1936) than with that of McLellan (1957) and show a greater constituent ratio of Central Atlantic Water than in areas to the east. Indeed, a few of the *Atlantis* station plots fall to the right of the Central Atlantic curve, but these points possibly represent errors in interpolation of salinity between the widely spaced sample depths. The majority of the 1965 and 1966 temperature–salinity values lay between those of the characteristic Coastal Water curve near its area of formation and those of the Coastal Water curve near its western limit of occurrence (Grampus station 10352, McLellan, 1957, fig. 6). The few values which fell in the proximity of the Slope Water curve were based on data from the isolated pools of relatively high temperature and salinity water at *Albatross IV* stations 9 and 22.

DISCUSSION

The cooling and warming of subsurface waters along the Continental Slope between Nova Scotia and Long Island are due to changes in the composition of these waters. Cold years occur when Slope Water is displaced or modified by Coastal Water of Labrador origin. Warm years occur when the Slope Water borders on the 200-m isobath and its constituent ratio of Coastal to Central Atlantic Waters is low. Bigelow (1927) pointed out that the relatively high temperature and salinity of the bottom water in the deep basins of the Gulf of Maine indicated its offshore origin. He concluded that this water, which enters the Gulf of Maine intermittently via the Northeast Channel, has its source along the slope of the Scotian Shelf and that the temperature and salinity variations of the deep water in the Gulf of Maine are due to fluctuations in the volume of, rather than in the temperature and salinity of, this inflowing drift. The more recent data presented in this paper demonstrate that the temperature–salinity characteristics of the subsurface waters adjacent to the mouth of the Northeast Channel vary; they are colder and less saline during periods of cooling than during periods of warming. Thus, it would appear that trends in subsurface temperatures within the Gulf of Maine can be traced to variations in the composition of these offshore waters as well as to the volume of their indraft through the Northeast Channel. This view is substantiated by the observations of L. M. Lauzier (unpublished) showing that in the deep waters in the Bay of Fundy and Emerald Basin, warming periods were accompanied by an increase in salinity and cooling periods were accompanied by a decrease.

Further evidence that the subsurface temperature trends observed within the Gulf of Maine are linked to variations in the composition of the subsurface waters bordering the Continental Shelf is afforded by the fact that the magnitude of the differences between 1955–60 and 1961–66 monthly mean temperatures was least in Area II. This area, which includes Murry and Wilkinson basins, is the most distant from the Northeast Channel. In addition, the

relatively shoal sill to the east of these basins further restricts horizontal communication with the open sea.

These subsurface data support the conclusion drawn from an analysis of temperature trends in the surface layers in the same area (Colton, 1968); that is, these temperature trends depend in large measure on the relative position and the degree of mixing of coastal and oceanic water masses. There is evidence to the effect that the changes observed in the relative position and degree of mixing of Coastal, Slope, and Central Atlantic waters along the Continental Slope are due to variations in atmospheric conditions that result from changes in the position and relative strength of the Icelandic Low. Lee et al. (1967) have postulated that surface temperature anomalies and their fluctuations over the Grand Banks and Georges Bank can be explained by advection caused by surface winds. Worthington (1964) has suggested that variations in barometric pressure as well as surface winds could cause advective movements of subsurface waters off the Scotian Shelf. It may be, however, that these advective movements of surface and subsurface water masses and the subsequent warming and cooling trends are more directly related to fluctuations in the strength of the North Atlantic Gyre, as suggested by Iselin (1940) and Stommel (1958). In this connection, an analysis of long-term trends in the volume transport of the Florida Current would be most useful.

Existing hydrographic and meteorological data are too fragmentary for a detailed study of long-term fluctuations in the distribution and degree of mixing of coastal and oceanic water masses in the area between Nova Scotia and Long Island. It is doubtful that adequate data for such an analysis will be available in the forseeable future. With existing instrumentation it should be possible, however, to monitor subsurface hydrographic conditions in a critical area such as the Northeast Channel. Such data, even if they consisted solely of time-series bottom temperatures, would greatly increase our capability to measure and predict trends in both subsurface and surface temperatures in the Gulf of Maine and contiguous waters.

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Atlantic Salmon Scales as Records of Spawning History[1]

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ABSTRACT

A female sea-run *Salmo salar* L. was caught in an experimental trap in East Apple River, Nova Scotia, during her upstream migration in October 1934. She was captured again in the same trap in 1935 and 1936. Counts of spawning marks on different scales from the same samples were inconsistent among themselves and with the history of the fish as shown by trapping records. Scale readings alone do not give a dependable estimate of the number of times a salmon has spawned if it has spawned two or more times.

METHODS

An experimental fish trap was operated on East Apple River, Nova Scotia (45°27′N lat, 64°49′W long) for three open-water seasons (1934–36) to study migrant salmon (White and Huntsman, 1938). Standardized handling of each captured salmon included measuring total length, with tail relaxed; taking a sample of scales from the "shoulder" position; attaching a strap-type, monel-metal tag (Rounsefell and Kask, 1945) to the anterior base of the dorsal fin; releasing each downstream migrant below the trap after handling and each upstream migrant above the trap.

REPEATED CAPTURES OF SAME FISH

A female salmon was captured October 29, 1934 and handled in the regular way. This same fish was taken again September 30, 1935 and October 8, 1936 — an almost, if not quite unique sampling sequence. Her lengths on these dates were 67, 71, and 77 cm and on all occasions she was in vigorous condition, the tag was firmly attached, and there was never any sign of inflammation of the flesh about the tag.

SCALE READINGS

Identifying Spawning Marks

In scale examinations, counts were made of spawning marks (regions of discontinuity of growth circuli) to determine the number of times salmon had spawned.

These marks develop in two stages: (1) while the fish in is freshwater, parts of the marginal growth circuli and parts of previous spawning marks,

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at and near the scale edge, may disappear ("erode"); and (2) when the fish returns to the sea and scale growth resumes, new marginal circuli are usually discontinuous with the eroded circuli. They do not join them and there is often an area of scar tissue between old and new circuli. These areas of disjunction are the spawning marks.

Spawning Mark Counts

The 1934 scales of the female mentioned above showed two spawning marks and marginal erosion indicating beginnings of a third mark (Fig. 1). She was therefore recorded as having spawned twice and as being on her third spawning migration.

The same number of spawning marks was recorded for 1935 scales when they were read. This anomaly was detected when 1934 and 1935 records were compiled during the winter of 1935–36 and the 1935 scale sample was re-examined. This showed that most 1935 scales had only two spawning marks, as previously recorded, but that a few had three (Fig. 2) as was expected from 1934 records. The record was therefore amended to indicate that in 1935 the fish was making her fourth spawning migration. And it was decided to keep a sharp lookout for her in 1936. When she was recaptured on October 8 a specially large scale sample was taken.

Many 1936 scales were "regenerated" and could not be read. All normal scales showed marginal erosion and were obviously in first stages of new spawning mark formation. Most normal scales showed only two clear previous spawning marks; several showed three but only one scale from the whole sample showed four spawning marks (Fig. 3). Four were expected because 1934 scales had shown two and some 1935 scales had shown three. Normal reading of a normal-sized, 1936 scale sample from this salmon would probably have resulted in a recording identical with that for 1934. But she was recorded as being on her fifth spawning migration because of the supplementary information.

DISCUSSION

If there were little annual scale growth and much erosion during a spawning period, one or more previous spawning marks and annual rings could be completely obliterated. This is what Blair (1937) found in working with scales of salmon of known age planted in freshwater Chamcook Lake. He found that ageings and counts of spawning marks were almost meaningless for these fish *after their first spawning*. Close to 70% of the age readings were wrong, some being 4 years less than known ages.

It is frequently stated that only small proportions of our sea-run salmon are multiple spawners, i.e., have completed more than one spawning migration (Kerswill, 1955; Jones, 1959) but the basis for distinguishing between multiple spawners that have spawned two, three, or more times has not been critically examined. Readings and re-readings reported here refer to scales from one

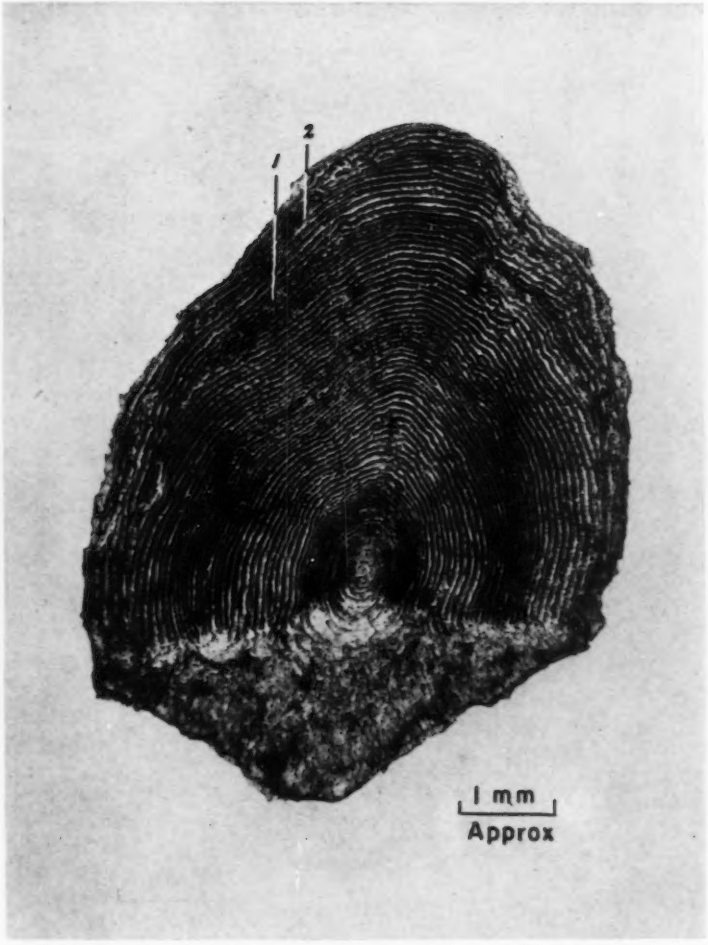

FIG. 1. 1934 scale with two spawning marks plus extensive marginal absorption at edge, the beginning of the third spawning mark (October 29).

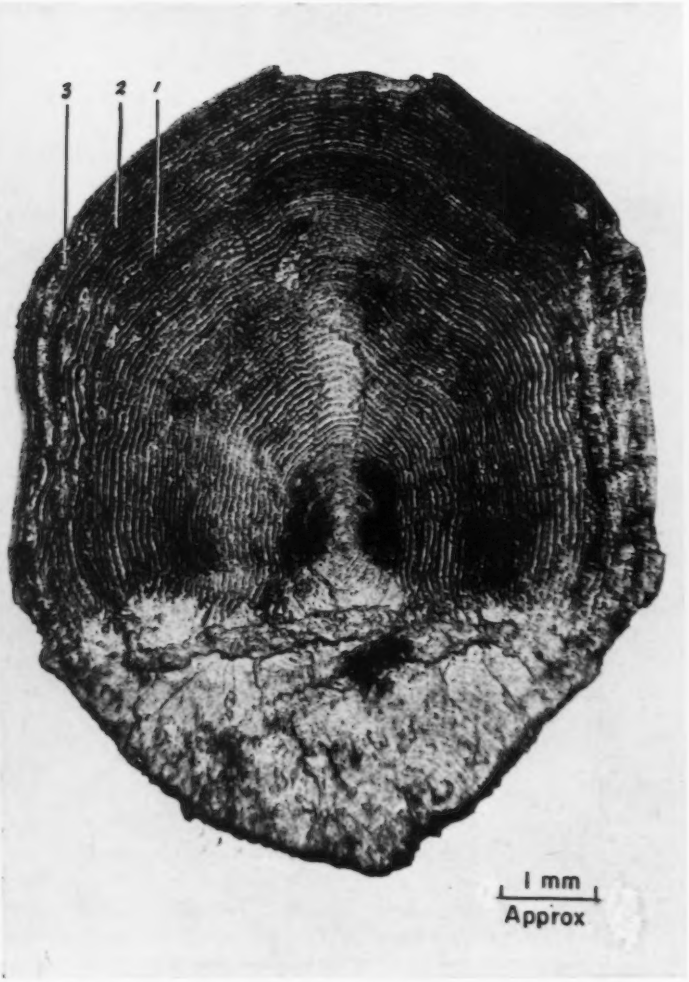

FIG. 2. 1935 scale showing three spawning marks and slight marginal absorption indicating beginning of fourth spawning mark (September 30).

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FIG. 3. 1936 scale showing four spawning marks and marginal absorption for a fifth mark (October 8).

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sea-run salmon from one river but it was no ordinary "one salmon." The information it provided was unique, for our coast, for testing reliability of spawning mark counts as indicators of spawning history of salmon. And in this case, "normal" determinations of numbers of spawnings beyond two were wrong in terms of what was known about the fish from trapping records. Elson (1966) emphasized the importance and need for this kind of information on individual fish to support or modify interpretations of their life histories from scale readings.

CONCLUSIONS

1. The count of spawning marks on a salmon's scale indicates only that that fish has spawned *at least* that number of times.
2. In our stocks there are probably more salmon that have spawned three or more times than would be supposed from scale readings alone.
3. Interpretations of salmon spawning histories from readings of scales of multiple spawners should be supported by whatever supplementary information can be marshalled on each fish.

ACKNOWLEDGMENTS

This paper is based on a draft prepared in 1954 by the senior author who had long experience in salmon scale reading.

We wish to thank Drs J. L. Hart and C. J. Kerswill for encouraging this delayed reporting and Dr P. F. Elson for assistance and helpful criticisms.

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Growth and Resistance to Stress in Brook Trout Fed Sublethal Levels of DDT[1,2]

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ABSTRACT

When underyearling brook trout (*Salvelinus fontinalis*) were fed DDT at a rate of 2.0 mg/kg per week for 31 weeks, they exhibited greater weight gain (43.2 ± 0.8 g) during the period than did untreated fish (36.6 ± 1.1 g). When underyearling fish were fed DDT at different rates for 26 weeks and then starved or fed at a rate equivalent to 10% of the usual feeding rate, the cumulative mortality during this period was 96.2% among fish exposed to 3.0 mg/kg per week, 88.6% among fish exposed to 2.0 mg/kg per week, and 1.2% among untreated fish. Differences in the length of survival of DDT-exposed fish occurred due to dosage, sex, and type of starvation. The evidence suggests that the mortality of DDT-exposed fish was due to the interaction of DDT residues with a combination of environmental stresses, namely starvation, decreasing water temperature, and possibly the physiological stress associated with the spawning season.

INTRODUCTION

The primary objectives of the investigations reported here were to determine whether chronic exposure to sublethal levels of DDT has a direct effect on growth of brook trout, and whether DDT-exposed fish are more susceptible to stress than are unexposed fish. An additional objective was to investigate the effect of frequency of exposure on the ability of brook trout to accumulate and metabolize DDT. I recently suggested that a weekly dosage of DDT applied in two feedings per week could be more efficiently metabolized, and consequently could be less toxic, than the same weekly dosage applied in one feeding per week (Macek, 1968).

Previous investigations of the effects of chronic exposure of fish to organochlorine insecticides have indicated that apparent increases in growth occurred in bluntnose minnows (*Pimephales notatus*) exposed to endrin (Mount, 1962), in cutthroat trout (*Salmo clarki lewisi*) exposed to DDT (Allison et al., 1964), and in male brook trout (*Salvelinus fontinalis*) exposed to DDT (Macek, 1968). Also it has been suggested that fish exposed to organochlorine insecticides were susceptible to stress such as starvation (Cope, 1961), decreasing water temperature (Elson, 1967), and spawning activity (Graham, 1960).

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MATERIALS AND METHODS

These investigations were carried out at the New Hampshire Fish and Game Department Powder Mill Rearing Station in New Durham, N.H. The chemical characteristics of the water at this station, the formulation and the source of the diet used, the feeding rates, and the methods of exposure, were previously described (Macek, 1968).

To study the effect of DDT on growth in brook trout, a group of 600 underyearling brook trout was supplied by the New Hampshire Fish and Game Department. These fish were randomly divided into eight experimental lots of 75 fish each and held in wooden troughs. Prior to the experiment, 25 fish in each experimental lot were anesthetized with 1:10,000 tricaine methanesulfonate (M.S. 222), and then weighed, measured, and tagged with metal jaw tags. Two of the experimental lots (average weight 30.2 ± 1.0 g) served as controls and were fed untreated feed, which was found to contain 0.36 ppm DDT (equivalent to a dosage of 0.05 mg/kg per week). The remaining six lots were fed DDT (technical grade, 77.2% *p,p'*isomer) at the rate of 2.0 mg/kg per week. Three of these treated lots (average weight 30.5 ± 0.9 g) received $\frac{1}{6}$ of the weekly dosage for six consecutive days each week; the other three lots (average weight 31.1 ± 1.1 g) received $\frac{1}{2}$ of the weekly dosage on the 1st and the 4th day of each week. The feeding period was from November 2, 1966 to June 8, 1967, a period of 31 weeks. Fish in each lot were weighed as a group, and the feeding rates adjusted accordingly, every 2 weeks. At the end of the exposure period individually tagged fish were weighed, measured, and sexed.

Three fish were removed from each experimental lot at the end of the exposure period. These, along with pretreatment samples were sent to the Wisconsin Alumni Research Foundation for moisture, fat, and residue analysis. Samples were dried in an air oven at 40–45 C for 36–48 hr. Dried samples were then ground with sodium sulfate and extracted in a Soxhlet apparatus with a mixture of 70 ml ethyl ether and 170 ml petroleum ether for 8 hr. After extraction the ethers were removed by evaporation on a steam bath. The fat was redissolved in petroleum ether and transfered to a volumetric flask. After making to volume, one half of the solution was pippeted into a tared beaker. The solvent was removed in a steam bath and the beaker dried in an air oven at 40–45 C for 3 hr. The beaker was reweighed and the percent fat calculated. The other half of the sample in the volumetric flask was washed onto a florisil column. DDT residues were eluted from the column with 5–95% and 15–85% (ethyl ether–petroleum ether) solutions. The respective solutions were taken to near dryness, and a known volume was injected into a Barber-Colman Pesticide Analyzer, Model 5360, equipped with an electron-capture detector.

To investigate the susceptibility of DDT-exposed fish to stress, a group of 800 underyearling brook trout, averaging 40.6 g, was provided by the New Hampshire Fish and Game Department. These were randomly divided into five equal lots and held in outdoor raceway pens. Two of these lots were un-

treated, two were fed DDT at 2.0 mg/kg per week, and the other at 3.0 mg/kg per week. Exposure was daily ($\frac{1}{6}$ weekly dosage/day) except for Sundays, from November 23, 1966 to May 19, 1967, a period of 26 weeks. At the end of this period, 80 fish from each of the three treatments were anesthetized, weighed, measured, and tagged with metal jaw tags. These were then divided into two groups each consisting of 40 fish from each treatment. One of these groups received no feed whatsoever. Although drastic reductions in available fish food often occur in nature after insecticide applications, complete starvation is unlikely to occur (Kerswill, 1967). Therefore, the other group was fed at a reduced rate of 6.5% of the amount recommended for moist feed (e.g. liver) for brook trout by Deuel et al. (1952). The date of death, weight, length, sex, and degree of sexual development was noted for each dead fish.

No mortality occurred during exposure of fish to DDT. Brook trout fed DDT exhibited no outward signs of distress or hyperexcitability, appearing as active, and accepting feed as readily, as the untreated fish.

Whole fish samples from the stress study were analyzed for insecticide residues at the Fish-Pesticide Research Laboratory in Columbia, Mo. Samples were extracted with 10% diethyl ether in petroleum ether. Clean-up involved partitioning with acetonitrile, followed by treatment with fuming sulfuric acid. Analysis was completed using a Varian Aerograph Model 200 gas chromatograph equipped with an electron capture detector.

The gains in weight and length of brook trout from the growth study were analyzed for differences due to treatments. Analysis of variance tested for main effects of dosage and sex. The results of the residue analyses and the determinations of body fat were also analyzed for differences due to treatments. Analysis of variance tested for differences in the length of survival of individual brook trout during starvation due to dosage, sex, and type of starvation. Methods used in all of the analyses were described by Steel and Torrie (1960). Differences between means were tested using Duncan's multiple range test, or a modification of this test to accomodate unequal subclass size (Kramer, 1956). Statistical significance was based on a probability of 0.05.

RESULTS

During the feeding period, the mean weight gain among fish was 36.6 $\pm$ 1.1 g for the untreated fish, 41.7 $\pm$ 0.8 g for fish exposed twice weekly, and 44.8 $\pm$ 0.8 g for fish exposed daily. All the differences were significant. The differences in weight gain between the sexes, and the interaction betwene treatment and sex, were not significant. The differences in gain in length among the experimental groups and between the sexes also were not significant. The total residues in DDT-treated fish were higher ($P \leq 0.05$) than those in untreated fish; also total residues in fish exposed daily were higher than those in fish exposed twice weekly (Table I). In fish exposed to DDT daily, the percent total residue present as DDT metabolites was higher ($P \leq 0.05$) than in the other two experimental groups. Differences in the percent body water and fat among the treatments were not significant.

TABLE I. Residue contents of whole brook trout (*Salvelinus fontinalis*) after being fed 2.0 mg DDT/kg per week for 31 weeks.

Sample	Weight	Total residues		% total residues		
		ppm fish	ppm fat	DDT	DDD	DDE
			Untreated[a]			
C-1	90.9	0.49	7.19	30.6	36.7	32.7
C-1	79.9	0.59	6.78	32.2	51.0	16.8
C-1	52.3	0.48	6.48	35.4	54.2	10.4
C-2	76.9	0.51	7.66	29.4	60.8	8.8
C-2	70.8	0.79	9.04	29.1	44.3	26.6
C-2	110.0	0.80	9.13	28.7	47.5	26.1
Mean	80.1	0.61	7.71	30.9	49.0	20.1
			Fed DDT daily			
D-1	78.1	19.8	222.5	13.0	74.4	12.6
D-1	70.0	16.6	178.5	10.2	72.3	17.5
D-1	83.8	13.8	146.5	26.0	61.0	13.0
D-2	73.5	11.8	170.7	8.4	73.3	18.3
D-2	105.8	12.3	130.1	12.2	71.5	16.3
D-2	101.9	11.2	138.8	8.0	76.8	15.2
D-3	77.9	13.4	156.5	14.2	70.9	14.9
D-3	72.2	13.6	165.0	8.9	76.4	14.7
D-3	122.0	12.3	120.6	19.6	65.0	15.4
Mean	87.2	13.8[b]	158.8[b]	13.4[b]	71.3	15.3
			Fed DDT twice/week			
TW-1	66.5	10.0	146.4	48.4	35.0	16.6
TW-1	61.3	10.8	143.9	50.8	36.9	12.3
TW-1	87.9	14.6	169.1	5.7	77.2	17.1
TW-2	67.4	9.5	119.7	12.6	74.8	12.6
TW-2	100.0	11.3	126.1	18.6	65.5	15.9
TW-2	104.2	12.0	133.0	36.7	51.6	11.7
TW-3	88.7	11.0	152.0	40.9	45.5	13.6
TW-3	90.2	10.2	130.2	29.3	58.5	12.2
TW-3	81.8	14.7	126.6	34.0	49.0	17.0
Mean	83.5	11.2[c]	138.5[c]	30.8	55.0	14.2

[a]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).

[b]Significantly different from untreated groups and groups exposed twice weekly at 0.05 level.

[c]Significantly different from untreated groups at 0.05 level.

During the 270 days of starvation, the cumulative mortality of brook trout (Fig. 1) was 1.2% among untreated fish, 88.6% among fish exposed to 2.0 mg/kg per week of DDT, and 96.2% among fish exposed to 3.0 mg/kg per week. No mortality occurred until the 20th week of starvation. Among

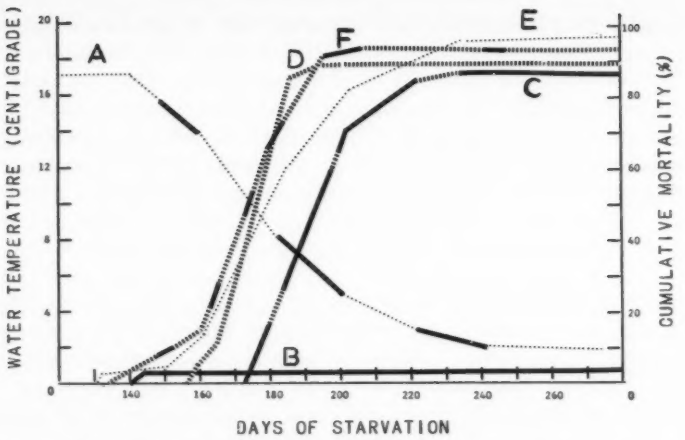

FIG. 1. Water temperature, and the cumulative mortality of brook trout previously fed DDT at the rate of either 2.0 or 3.0 mg/kg per week for 26 weeks, during the period of starvation or reduced feeding. LEGEND: A, temperature; B, untreated; C, 2.0 mg (reduced feeding); D, 2.0 mg (starvation); E, 3.0 mg (reduced feeding); F, 3.0 mg (starvation).

the DDT-treated fish, the average length of survival of brook trout exposed to the higher dosage (176 days) was less ($P \leq 0.05$) than that of those exposed to the lower dosage (187 days); that of males (176 days) was less than that of females (185 days); and that of fish completely starved (177 days) was less than that of partially starved fish (186 days). The interaction among dosage, sex, and type of starvation was not significant.

The DDT-treated brook trout which were completely starved (Table II) exhibited a mean decrease in body weight of 29.1% from the beginning of

TABLE II. Parts per million total residues in whole brook trout (*Salvelinus fontinalis*) subjected to starvation, and the percent weight loss during the starvation period.

Treatment	No.	Starvation	ppm DDT[a]	% loss
Untreated[b]	2[c]	Complete	0.36	26.0
Untreated	1[c]	Partial	0.25	None
2.0 mg/kg per week	2	Complete	45.8	31.0
2.0 "	2	Partial	20.2	None
3.0 "	2	Complete	42.6	26.0
3.0 "	1	Partial	29.6	None

[a]Includes *o,p'*-DDT, *p,p'*-DDT, DDD, and DDE.
[b]Untreated feed contained 0.36 ppm DDT (equivalent to 0.05 mg/kg per week).
[c]Fish still alive when taken for analysis.

the starvation period until death. The mean body weight of partially starved fish did not decrease during this period. The results of the residue analyses of fish from this experiment suggest that the weight loss in completely starved fish probably resulted in an increase in the concentration of DDT residues. The beginning of appreciable mortality coincided with the beginning of the period of decreasing water temperature; the bulk of the mortality occurred during the period from 165 to 195 days after starvation began (Fig. 1).

DISCUSSION

In each of the previous investigations in which observations were made of the effects of organochlorine insecticides on group of fish (Mount, 1962; Allison et al., 1964; Macek, 1968), the possibility existed that the observed differences between treated and untreated fish were either due to random variation or selective mortality or sampling among the test population. However, in this investigation, the observed differences in weight gain between treated and untreated fish could not have been due to any of the above factors, and were considered to be a direct result of exposure to DDT. In an earlier investigation (Macek, 1968), I observed an apparently sex-limited increase in the growth of male brook trout exposed to DDT, and suggested that such an increase may not have occurred in DDT-exposed females because sufficient DDT was isolated in developing ova to preclude such an effect. That exposure to DDT had the same effect on immature males and females in this investigation, lends support to this hypothesis.

The occurrence of higher total residues in fish exposed to DDT daily than in fish exposed twice weekly could indicate either a more efficient uptake of the insecticide by fish in the former group, or more efficient insecticide metabolism and excretion in the latter group, or both. The presence of a higher percent of DDT metabolites in samples of fish fed DDT daily suggests that these fish more efficiently metabolized DDT than did those fish in groups fed twice weekly. Wedemeyer (1968) has reported that DDT metabolism in fish consisted in dechlorination by both the liver microsomal enzyme system and the intestinal microflora. Morello (1965) reported that the in vitro metabolizing capacity of rat liver microsomes was apparently increased only 72 hr after in vivo exposure to DDT. Assuming a similar enzyme response could occur in fish, it is possible that the more frequent exposure could maintain the increased level of enzymatic activity more efficiently than the less frequent exposure, resulting in the higher percent of DDT metabolites in fish exposed daily. The evidence from this study indicated that the use of a weekly dosage rate, without sufficient information regarding specific methods and frequency of application, is inadequate for reporting and comparing independent investigations of fish–pesticide relationships.

There is, of course, the possibility that the DDT-exposed fish in the stress experiment would have died even if they had not been stressed, and it is unfortunate that a positive control (i.e. DDT-exposed fish fed at a normal

rate) was not included in this investigation. However, the susceptibility of insecticide-exposed animals to additional stress is well documented for higher vertebrates, and has been suggested for fish (Cope, 1961). As early as 1947, Fitzhugh and Nelson showed that rats exposed to DDT exhibited marked tremors when they were deprived of food. Dale et al. (1962) demonstrated clearly the processes occurring during the starvation of DDT-exposed rats. They showed a rapid reduction in body weight, an increased concentration of DDT and DDE in the fat, and increases in the concentrations of these compounds in other tissues, indicating that an equilibrium was maintained. Bernard (1963) stated that when DDT-treated birds were starved, fat was metabolized and DDT was transfered to more vital areas such as the brain.

The DDT-treated brook trout which were not fed exhibited a decrease in body weight (mean of 29.1% at death) and an apparent increase in the concentrations of DDT residues (Table II). In addition they survived an average of only 183 days as compared with 98.7% survival of untreated fish after 270 days. These observations suggested that mobilization of DDT residues, similar to that described during the starvation of higher vertebrates, occurred in these fish and resulted in the observed mortality. However, other observations suggest that starvation probably was not the sole stress involved in producing the mortality among DDT-treated fish. For example, although the insecticide-exposed fish which were partially starved survived an average of only 192 days, they exhibited a mean decrease in body weight of only 0.8% at death, suggesting that in this group total body fat was not appreciably decreased and residue concentrations apparently were not increased. Also the similarity in the mean length of survival of partially and completely starved fish receiving the high DDT dosage (178 and 174 days respectively) indicated the mortality in this group probably was not due to the stress of starvation alone. Probably a combination of stresses, of which starvation may or may not have been the most important, was responsible for the mortality of DDT-exposed brook trout in this study.

That appreciable mortality did not occur until the water temperature began to decrease (Fig. 1) suggested decreasing water temperature may have been an additional source of stress. Metcalf (1955) described reports of higher percent mortality of insects exposed to DDT occurring at lower temperatures than at higher temperatures. Cope (1965) reported that a similar phenomenon occurred in rainbow trout exposed to DDT for 24 hr. Ogilvie and Anderson (1965) suggested that DDT may interfere with normal thermal acclimation mechanisms.

A large portion of the mortality among DDT-exposed brook trout occurred during November, the period when brook trout are usually ripe at Powder Mill, suggesting that perhaps the physiological state associated with spawning was another source of stress. Graham (1960) reported that, after summer spraying of Montana forests with DDT, delayed mortality of game fish, apparently associated with spawning activity, occurred in the late fall and early winter. Allison et al. (1964) reported that losses among DDT-exposed

cutthroat trout after spawning were greater among females from the high dosage lots than among those from the low doasge lots or controls.

Information concerning the significance of insecticide residues in fish, or the hazard posed by such residues to fish, is presently lacking in the literature. The results of this investigation conclusively indicate that DDT residues in fish pose a definite hazard to the existence of the organism. Significantly, the combination of stresses suggested as a cause of the DDT-related delayed mortality frequently occurs in nature. In areas treated with insecticides, a paucity of fish food organisms often may be characteristic of waters during late fall and early winter. Temperature, of course, generally decreases during this time of the year. Under such conditions, populations of fall and winter spawners in areas recently treated with insecticides could suffer considerable mortality due to the interaction of insecticide residue and multiple environmental stresses.

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Significance of Dimethyl Sulfide to the Odor of Soft-Shell Clams[1,2]

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ABSTRACT

In 12 samples of fresh soft-shell clam meats which were collected over their spawning period, the average concentration of dimethyl sulfide (DMS) was 3 ppm. Odor evaluations were made to determine the range of concentration of pure DMS that a panel recognized as a clamlike odor. Since the concentration of DMS in our clam samples was within this range (0.08–40 ppm), it is suggested that DMS dominates the odor of fresh soft-shell clams.

RÉSUMÉ

Dans 12 échantillons de viande fraiche de mye recueillis durant la période du frai, la concentration moyenne de sulfure dimethyle (DMS) fut 3 ppm. Des évaluations d'odeur furent faites pour déterminer l'étendu des valeurs de concentration de DMS pur reconnues par un jury comme étant semblable à l'odeur de mye. Etant donnée que la concentration de DMS de nos échantillons de mye était à l'intérieur de cette étendue de valeurs (0.08–40 ppm), l'on suggère que le DMS domine l'odeur de mye fraiché.

INTRODUCTION

Dimethyl sulfide (DMS) has been isolated from a variety of fishery products. It has been described as the most abundant sulfur compound of fresh Pacific oysters (*Crassostrea gigas*) (Ronald and Thomson, 1964) and fresh soft-shell clams (*Mya arenaria*) (Mendelsohn and Brooke, 1968). DMS has been discovered in volatile mixtures obtained from refrigerated haddock (*Melanogrammus aeglefinus*) (Mangan, 1959), cod (*Gadus morhua*) (Wong et al., 1967), and several species of marine phytoplankton or zooplankton (Ishida and Kadota, 1967; review by Challenger, 1959; review by Ackman et al., 1966c). Cooking or heat processing increases the concentration of DMS in seafood (Ackman et al., 1966a; Hughes, 1964). High concentrations of DMS have been associated with off-flavors such as "petroleum odor" in certain lots of canned chum salmon (Motohiro, 1962), a "blackberry odor" in certain landings of fresh cod (Ackman et al., 1967; Sipos and Ackman, 1964) and other species of groundfish (Lippa, 1965; review by Ackman and Hingley, 1968). In general, these off-odors are caused by postmortem breakdown of unusually large amounts

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of dimethyl-beta-propiothetin (DMPT) which has accumulated in the flesh (Ackman et al., 1966a) as a result of heavy feeding by the fish on certain species of marine plankton which contain DMPT (Lippa, 1965; Tocher et al., 1966; Ackman et al., 1966b; Craigie et al., 1967).

DMPT is believed to be the most significant precursor of DMS in fresh soft-shell clam meats. Modest DMPT levels have been reported in clam samples obtained near Prince Edward Island (Ackman and Hingley, 1968). DMPT can be converted to DMS enzymatically in phytoplankton (review by Challenger, 1959; discussion by Ackman and Hingley, 1968). Although this enzyme system is present in fish liver (Motohiro, 1962) it is apparently not present in muscle tissue since the amount of DMPT which is present at time of death changes only slightly during chill-storage (Motohiro, 1962; Ackman and Hingley, 1968). However, DMPT can be converted into DMS and acidic products by heating, or even by an isothermal increase in *p*H of the tissue (Ackman et al., 1966a; Motohiro, 1962). For example, the formation of DMS by adding cold concentrated alkali is rapid enough to allow the use of this reaction to determine the DMPT concentration in seafoods or plankton (Ackman and Dale, 1965). Heat is necessary for the formation of DMS from other components such as methionine (Brooke et al., 1964; review by Hughes, 1964) but DMPT appears to be a more significant precursor of DMS in raw or cooked soft-shell clam meats.

During the course of our previous study (Mendelsohn and Brooke, 1968), we found that DMS was the dominant volatile component in all of our soft-shell clam samples and that the odor of the effluent stream from the gas chromatographic column resembled the odor of soft-shell clams when the component later identified as DMS was being eluted. In that study, we also found that passage of a sample of clam volatiles through mercuric chloride solution removed its volatile sulfides as well as its odor of soft-shell clams. The present investigation was undertaken to determine; (1) the concentration of DMS in soft-shell clam meats; and (2) whether this concentration of chemically pure DMS resembles the typical odor of soft-shell clam meats.

EXPERIMENTAL

Collection of DMS Sample from Clams

Two methods were used to measure DMS in clam meats. In both methods, a total volatile condensate (TVC) was collected (Mendelsohn and Brooke, 1968) from fresh raw Essex clams (Gadbois et al., 1967) as described earlier. These methods differed from each other in the preparation of a DMS sample for gas chromatography (GC).

The head-gas method for removing a sample of DMS from the TVC was based on expanding the vapor (head-gas) above the TVC into a known volume. Then a measured aliquot of this head-gas was removed for GC analysis by way of a transfer trap. The transfer apparatus shown in Fig. 1 is operated in the following manner. With all glassware at room temperature and the stopcock

from the TVC container (I) closed, the entire transfer system is evacuated to a pressure of 1 μ. The head-gas from I is then expanded into manifolds G, F, and H and allowed to equilibrate for 20 min. After closing the lower stopcock to F, the aliquot in F is expanded and equilibrated to a choice of volumes including A, B, C, D, and E in different combinations. (In most of the analyses A and B were used.) Aliquots of known volume and pressure were removed (usually from B) and condensed in E by immersing this transfer trap in liquid nitrogen. Then the trap was disconnected from the glass apparatus and attached to the GC sampling port.

The stripping method of treating the TVC to remove DMS was based on Meirs' (1966) procedure. A stream of nitrogen gas was passed through both the liquid and vapor phases of the TVC which had been collected in a modified receiver (Fig. 2). After leaving this container, the nitrogen stream (which now contained the volatile components) passed through the following sequence of reagents: (1) two calcium chloride tubes to collect moisture; (2) lead acetate solution to trap hydrogen sulfide; (3) concentrated sulfuric acid to remove the remaining volatile sulfides; and (4) liquid nitrogen to trap remaining volatile compounds. After disconnecting the sulfuric acid trap from the apparatus, its solution was diluted with cold water to reduce the solubility of DMS. An aliquot of the vapor phase in this container was removed for GC analysis.

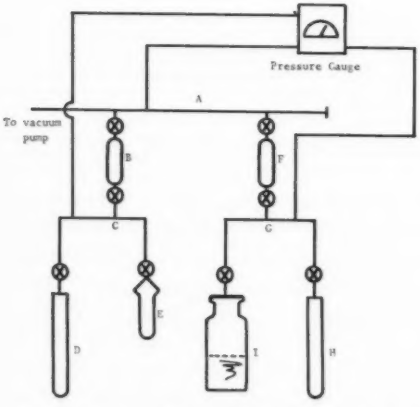

FIG. 1. Diagram of high vacuum apparatus used for determination of hydrogen sulfide. A = high vacuum line; B, F, C, and G = glass manifolds; D and H = gas bottles; E = transfer trap; I = total condensate container.

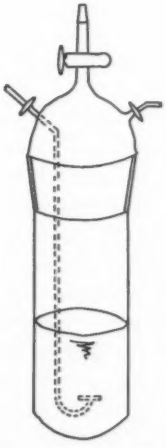

FIG. 2. Modified receiver for a total volatile condensate used for subsequent collection of sulfur compounds by a stripping method.

Gas Chromatographic Analysis

The concentration of DMS in the sample obtained by either the head-gas method or the stripping method was determined by GC (Mendelsohn and Brooke, 1968). To calculate the concentration of DMS in the sample, the area of its peak on a chromatogram was measured. Then this area was compared with the areas obtained by chromatographing known concentrations of pure DMS. Two standard curves were constructed for this purpose.

To establish a standard curve for the head-gas method, a few drops of pure DMS (Matheson, Coleman & Bell No. 7825) were transferred to a test tube fitted with a standard taper joint. The test tube was attached to the apparatus (Fig. 1) and its contents frozen in liquid nitrogen. After evacuating the system to 1 μ, the DMS was allowed to warm up to 25 C. Various concentrations of the head-gas were expanded into B which had a volume of 39 ml and equilibrated at different pressures. The various amounts of DMS were transferred to E and determined by GC. Since each sample's pressure, volume, and temperature were known, the concentration of DMS was calculated and related to peak area on its GC curve.

The second standard curve, based on the stripping method of collecting DMS, used a gas-tight syringe to inject a sample into the GC. For this purpose a DMS stock solution was prepared by dissolving 1.0 ml of reagent in 99.0 ml of reagent grade concentrated sulfuric acid previously chilled to 1 C. Then a series of DMS standards was prepared by placing aliquots of the cold stock solution and cold distilled water (1 C) in 25-ml Erlenmeyer flasks with serum caps. Just before a GC analysis, each solution was warmed to 25 C, and a 400-μliter aliquot of the head-gas was removed by a gas-tight syringe and injected into the GC.

The efficiency of each method in extracting DMS from the TVC was checked by analyzing the liquid phase of the TVC after completing a collection. For this purpose, an aliquot of the liquid phase of the TVC was analyzed by a GC equipped with a hydrogen flame detector which is relatively insensitive to water. No DMS was found in these samples under conditions which enabled detection of 1 ppm DMS.

Both the head-gas method and the stripping method of collecting DMS from the TVC proved effective. However, the head-gas method was used for most of the analyses because it is simpler, more convenient, and, for the purpose of this investigation, just as accurate. These points were verified in preliminary work by using both methods of collection on the same sample of clams.

Odor Evaluations

An untrained panel of laboratory personnel cooperated in a series of odor evaluations. The personnel were presented with 10–20 solutions (at 25 C) containing various known concentrations of pure DMS in either distilled water or light mineral oil. Each panelist was asked to judge the odor of a control (solvent only) then judge the odor of vials which contained increasing concentrations of DMS in sequence. The panelists were asked to answer:

(1) which was the first vial in which a recognizable clamlike odor was found (threshold DMS concentration resembling clam odor); and (2) in which vial was the odor no longer clamlike (maximum DMS concentration resembling clam odor).

RESULTS AND DISCUSSION

The concentrations of DMS in the 12 clam samples examined are given in Table I. The principal source of variability in these results is believed to be due to the clam samples themselves instead of the analytical procedure.

TABLE I. Dimethyl sulfide content of soft-shell clam meats.

Sample code[a]	Dimethyl sulfide content (*ppm*)
4-1	2.88
4-2	4.55
5-1	5.64
5-2	5.26
5-3	2.04
5-4	2.08
5-5	1.94
5-6	4.54
5-7	0.74
5-8	1.04
6-1	0.20
6-2	0.21
Mean and its standard deviation: 2.59±2.77 ppm	

[a]For example, 4-1 refers to April 1.

Although all of these samples were very fresh, they were collected during the clam's spawning season (April to June) — a period in which their feeding habits change. This contention is supported by our observation that three times as much DMS was found in the viscera than in the muscle tissue of a clam sample collected from the same bed in October of the previous year and by the conclusion of Ackman and Hingley (1968) that the precursor of DMS, DMPT, is part of the normal diet of soft-shell clams.

By comparing data from the analysis of soft-shell clam meats (Table I) with the results of odor evaluations in Table II, it is evident that the concentration of DMS found in clams is within the range of concentrations of pure DMS said to have a typical "clamlike" odor by the panel. It should be emphasized that the values in Table II are based on recognition of a clamlike odor by the panelists since the odor threshold of DMS in water is only 0.33 (±0.02) ppb (Guadagni et al., 1963). Similarly, the higher values for DMS in oil are probably due to DMS being more soluble in oil than in water.

TABLE II. Recognition of dimethyl sulfide as the odor of soft-shell clams.

Solvent used	Threshold concentration for recognition of clamlike odors[a]	Maximum concentration in which a clamlike odor was recognized[a]
Water	0.079±0.075	40±42
Mineral oil	1.2±1.0	310±270

[a]Dimethyl sulfide concentrations expressed in ppm of solvent used. Values given are the mean and its standard deviation of each type of evaluation performed.

Since DMPT is a common ingredient in the diet of several species of bivalves (Ackman and Hingley, 1968), it is not surprising that DMS has been designated as the odor of fresh oysters (Ronald and Thomson, 1964) as well as soft-shell clams. In contrast to these species, other bivalves contain negligible amounts of DMPT (Ackman and Hingley, 1968) and the ocean quahog (*Arctica islandica*) is one of this group which also contains a negligible amount of DMS in its aroma (J. M. Mendelsohn, unpublished observations). Although organoleptic differences between species of bivalves include other factors such as taste, texture, color, method of preparation, and serving, it is suggested that DMS is the most significant component in the odor of those bivalves which ingest and retain large amounts of DMPT.

Although this investigation was limited to fresh, raw, soft-shell clams, other results (Mendelsohn and Brooke, 1968) show that DMS dominates the composition of volatile mixtures obtained from stored, cooked, or radiopasteurized clam meats. On the basis of these results, it appears that DMS also dominates the odor of clams which received these treatments. In the case of stored samples, it is possible that microbial degradation of methionine (Dunham et al., 1968) as well as some decomposition of DMPT (Ackman et al., 1966a; Motohiro, 1962) is responsible for the DMS observed in that study.

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Distribution of ^{65}Zn In Tissues of Two Marine Crustaceans Determined by Autoradiography[1]

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ABSTRACT

In the benthic amphipod *Anonyx* sp., and the euphausiid *Euphausia pacifica* Hansen, ^{65}Zn accumulated from seawater was shown by autoradiography to be localized predominantly in the exoskeleton and interstitial spaces of the myofibrils. Also, the gut and hepatopancreas of *Anonyx* sp. and the eye of *E. pacifica* contained ^{65}Zn. The presence of ^{65}Zn in crustacean exoskeletons may affect the efficiency of transfer of ^{65}Zn through the food web and the vertical distribution of ^{65}Zn in the Pacific Ocean along the Oregon coast.

INTRODUCTION

We have used the technique of autoradiography to determine the distribution of ^{65}Zn in tissues of the benthic amphipod *Anonyx* sp.[5] and the euphausiid *Euphausia pacifica* Hansen. To date, the study of the distribution of both radioactive and stable elements in tissues of aquatic crustaceans has been limited to the larger decapods (Vinogradov, 1953; Bryan, 1961, 1964, 1965, 1967a; Hiyama and Khan, 1964; Hiyama and Shimizu, 1964; Polikarpov, 1966; Sather, 1966). The methods used by these investigators to describe elemental distribution were the same as those used for fish and mammals, i.e., dissection and analyses of individual body parts. This approach has little applicability to small crustaceans, such as euphausiids and amphipods, because dissection and accurate elemental analyses are extremely difficult. The use of autoradiography, which can be either qualitative or quantitative, allows one, however, to determine the presence of a radionuclide in animal tissue without dissection.

Recently both *Anonyx* sp. and *E. pacifica* have been the subject of laboratory investigations dealing with the metabolism and cycling of ^{65}Zn in the marine environment. Uptake and elimination rates of ^{65}Zn as affected by

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[5]*Anonyx* sp. is a new species and is currently being described by Dr J. Laurens Barnhard of the U.S. National Museum using specimens from our collections.

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food, temperature, and sediment have been determined for *Anonyx* sp. (Cross, MS, 1968; Cross et al., 1968) and similar rates have been determined for *E. pacifica* with regard to temperature and concentrations of ^{65}Zn in sea water (Fowler et al., 1968). The purpose of this paper is to describe the distribution of ^{65}Zn in tissues of *Anonyx* sp. and *E. pacifica* by the use of autoradiography.

METHODS

The experimental animals were captured in neritic waters off the Oregon coast during the summers of 1965 and 1966. The amphipods were collected with baited traps placed on the bottom at depths of 80–120 m, whereas euphausiids were obtained by towing a ½-m net to a depth of 3 m at night. All animals were transported alive to the Battelle Northwest Laboratory in Richland, Washington, where the experiments were conducted.

The two species were held in separate containers at 7–10 C in membrane-filtered (0.45 μ pore size) sea water containing 25 μCi ^{65}Zn/liter and an average concentration of stable Zn of approximately 20 μg/liter. After 8 days in the radioactive water, the animals were removed, preserved in 10% buffered formalin, imbedded in paraffin, and sectioned with a microtome. Autoradiographs were prepared by dipping de-paraffinized slides of the animal tissue into a liquid nuclear tract emulsion (a mixture of equal portions of Ilford K-5 Nuclear Tract Emulsion,[6] in gel form, and distilled water). The slides were then placed in light-tight boxes in a refrigerator at 5 C, and left for about 3 weeks until the emulsion was exposed. The emulsion was developed in Kodak D-19 developing solution, and the slides were stained with haemotoxylin and eosin. This technique is a modification of a method described by Novek (1962).

DISTRIBUTION OF ^{65}ZN IN TISSUES OF *ANONYX* SP.

Autoradiographs of amphipods that accumulated ^{65}Zn from sea water showed that the exoskeleton was a predominant site of localization of ^{65}Zn. The ^{65}Zn in the exoskeleton appeared to have penetrated into the inner layers (Fig. 1A). Zinc-65 was present also in most of the cracks and fissures of the outer portion of the exoskeleton. Thus, a portion of the exoskeleton may be permeable to zinc. Little is known about the crustacean exoskeleton, except that it exhibits varying degrees of permeability to water and salts in the environment (Dennell, 1960).

Another area of high concentration of ^{65}Zn was muscle tissue. Here much of the radionuclide apparently is restricted to interstitial spaces of the myofibrils (Fig. 1B) — an indication that part of the body burden of ^{65}Zn is in the body fluids. This observation agrees with results obtained by Bryan (1964) who found that changes in the concentration of zinc in the muscle of the lobster *Homarus vulgaris* varied with changes in the concentration of zinc in blood located in the extracellular spaces. Also, muscles that can contract quickly

[6]Trade names referred to in this publication do not imply endorsement of commercial products.

have less zinc than slow-contracting muscles, and muscle-to-blood ratios for ^{65}Zn in "slow" muscle are roughly double those for "fast" muscle (Bryan, 1967b). Bryan suggested that "slow" muscle is the more permeable to zinc; if musculature in amphipods is comparable with that in decapods, the muscle of *Anonyx* sp. in Fig. 1B may be fast-contracting muscle because very little ^{65}Zn has penetrated into the muscle tissue.

Some ^{65}Zn was present in the gut (Fig. 1C) and in the hepatopancreas (Fig. 1D). Because ^{65}Zn was accumulated directly from filtered sea water by the amphipods, the presence of this radionuclide in the gut could not be due to absorption from radioactive food, unless bacteria were available as a source of nutrition. If *Anonyx* sp. swallows sea water, the presence of ^{65}Zn in the gut would not be surprising. Bryan (1964) stated that when the lobster *H. vulgaris* was exposed to sea water of high stable zinc content (100 μg per liter), much of the accumulated zinc was taken up in the hepatopancreas but very little by the gut. Comparison of our data with Bryan's may not be completely valid because the lobsters he used were exposed to sea water longer (15–43 days) than the exposure period for *Anonyx* sp. (8 days).

DISTRIBUTION OF ^{65}ZN IN TISSUES OF *EUPHAUSIA PACIFICA*

The distribution of ^{65}Zn in exoskeleton and muscle tissue of *E. pacifica* was similar to that already described for *Anonyx* sp., i.e., ^{65}Zn was present on the outer surface of the exoskeleton (Fig. 2A) and in the interstitial areas around the myofibrils (Fig. 2B). The musculature shown in Fig. 2B, from the dorsal cephalothoracic region, contained small amounts of ^{65}Zn, and might be "fast" muscle. Fowler et al. (1968) reported that body fluids lost during dissection of internal tissues of euphausiids accounted for about 17% of the total body burden of ^{65}Zn.

Autoradiographs gave no evidence of ^{65}Zn in the gut of euphausiids. The canals of the hepatopancreas, however, showed some traces of ^{65}Zn (Fig. 2C) which might have entered there via the gut, or by absorption from the blood after absorption through the gills. It is not known whether *E. pacifica* swallows significant amounts of water.

The eye of *E. pacifica* contained ^{65}Zn along both sides of the cornea and along the outer surface of the lens (Fig. 2D). Zinc-65 has been detected also in the eye of a fin whale, *Balaenoptera physalus* (Osterberg et al., 1964c), and in the eyes of several species of freshwater fish taken from the Columbia River (Watson, 1966). Leiner and Leiner (1944) reported the presence of stable zinc in the eyes of both freshwater and marine fish. Retention of ^{65}Zn in the eyes of *E. pacifica* may be of little quantitative significance, however, because these organs accounted for only 4% of the total body burden in this species (Fowler et al., 1968).

ECOLOGICAL IMPLICATIONS

The distribution of elements in tissues of marine crustaceans may have ecological as well as physiological significance and may affect the efficiency

with which the elements are transferred through the food web. Elements sorbed to exoskeletal material might not be as readily assimilated by a consumer as those located in body fluids or bound to muscle or internal organs. Indirect evidence indicates that the method by which ^{65}Zn is accumulated by *Anonyx* sp. and *E. pacifica* affects the fraction of ^{65}Zn associated with the exoskeleton. In experiments measuring elimination rates of ^{65}Zn in *Anonyx* sp., Cross et al. (1968) found that the fraction of the ^{65}Zn lost at molting was about 20% of the total body burden when accumulation had been directly from filtered sea water and only 2% when accumulation had been from food (*Artemia*). Similarly, in *E. pacifica* the loss of ^{65}Zn at molting was about 18% when accumulation was from filtered sea water (Fowler and Small, 1967) and only 1% when accumulation was from ingestion of labeled *Artemia* (S. W. Fowler, L. F. Small, and J. M. Dean, unpublished data). These differences in the loss of ^{65}Zn at molting appear reasonable since accumulation of ^{65}Zn from water should result in a larger fraction of the total body burden sorbed to the exoskeleton than if accumulation had been from food.

Molting by large populations of *E. pacifica* also might play a significant role in the vertical distribution of ^{65}Zn along the Oregon coast. During the summer months this region receives the waters of the Columbia River, which contain significant amounts of ^{65}Zn as a result of the Hanford Atomic Operations plant in Richland, Washington. *Euphausia pacifica* often represents the largest biomass of macroplankton in Oregon coastal waters (Osterberg et al., 1964a) and serves as forage for a variety of marine animals including the lanternfish, *Lampanyctus leucopsarus* (Osterberg et al., 1964b); coho salmon, *Oncorhynchus kisutch* (Kujala et al., 1968); and the baleen whale, *Balaenoptera physalus* (Osterberg et al., 1964c). In addition, *E. pacifica* undergoes diel vertical migrations, ranging from the surface at night to greater than 200 m during the day (Osterberg et al., 1964a), and therefore is available to mesopelagic as well as epipelagic predators. Fowler and Small (1967) postulated that sinking exoskeletons of *E. pacifica* could significantly affect the vertical distribution of ^{65}Zn along the Oregon coast, since these organisms have a molting frequency of about 5 days. Because of the benthic habits of *Anonyx* sp., however, molted exoskeletons of this species would concentrate near the bottom and not affect the vertical distribution of ^{65}Zn.

We have demonstrated that autoradiography is a useful means by which knowledge of elemental distribution can be gained. Although the autoradiographs presented in this study were not analyzed quantitatively, they do give an insight into the relative capacities of various tissues to concentrate ^{65}Zn directly from sea water. If we assume chemical similarity between ^{65}Zn and stable zinc, relative concentrations of the stable isotope in various tissues are also indicated by the method.

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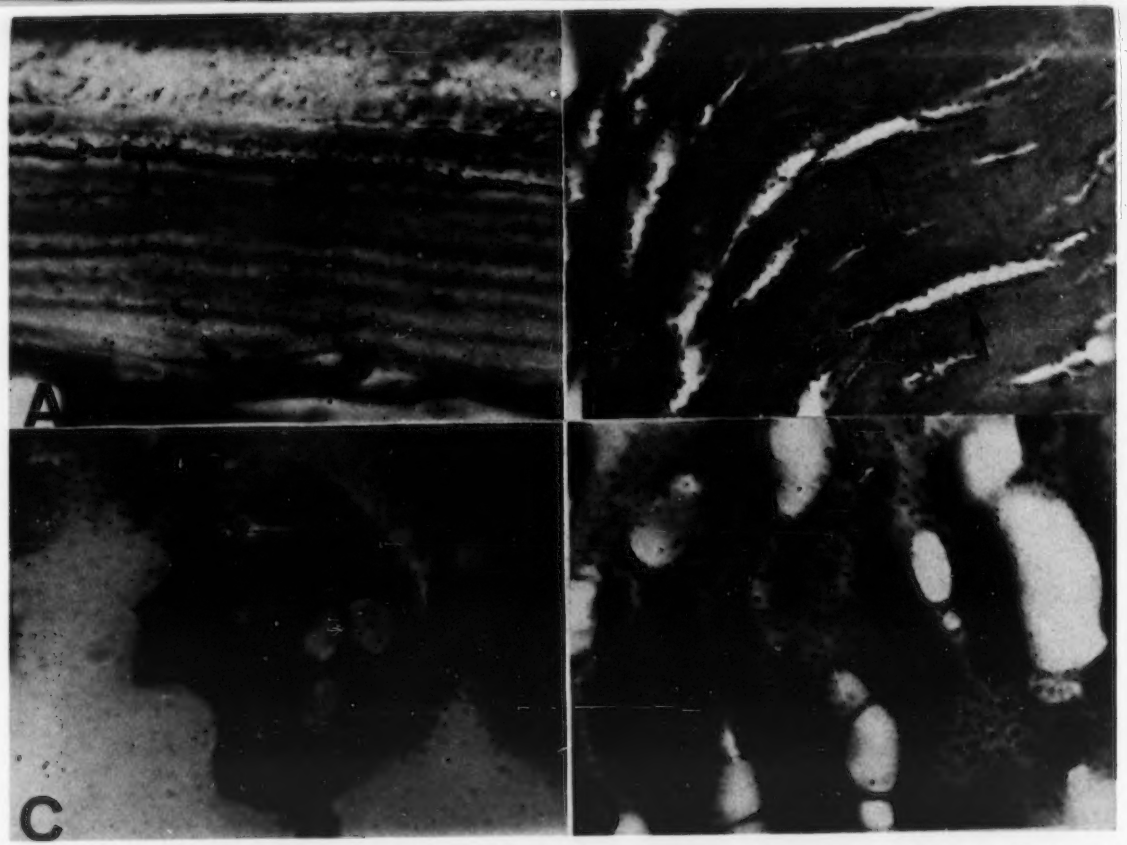

FIG. 1. Autoradiographs (400×) showing the presence of ^{65}Zn in *Anonyx* sp. for (A) exoskeleton, (B) muscle, (C) gut, and (D) hepatopancreas. The presence of ^{65}Zn is shown by the darkened areas in the exoskeleton and along the interstitial spaces of muscle (see arrows), and by the scattered black dots in the gut and hepatopancreas.

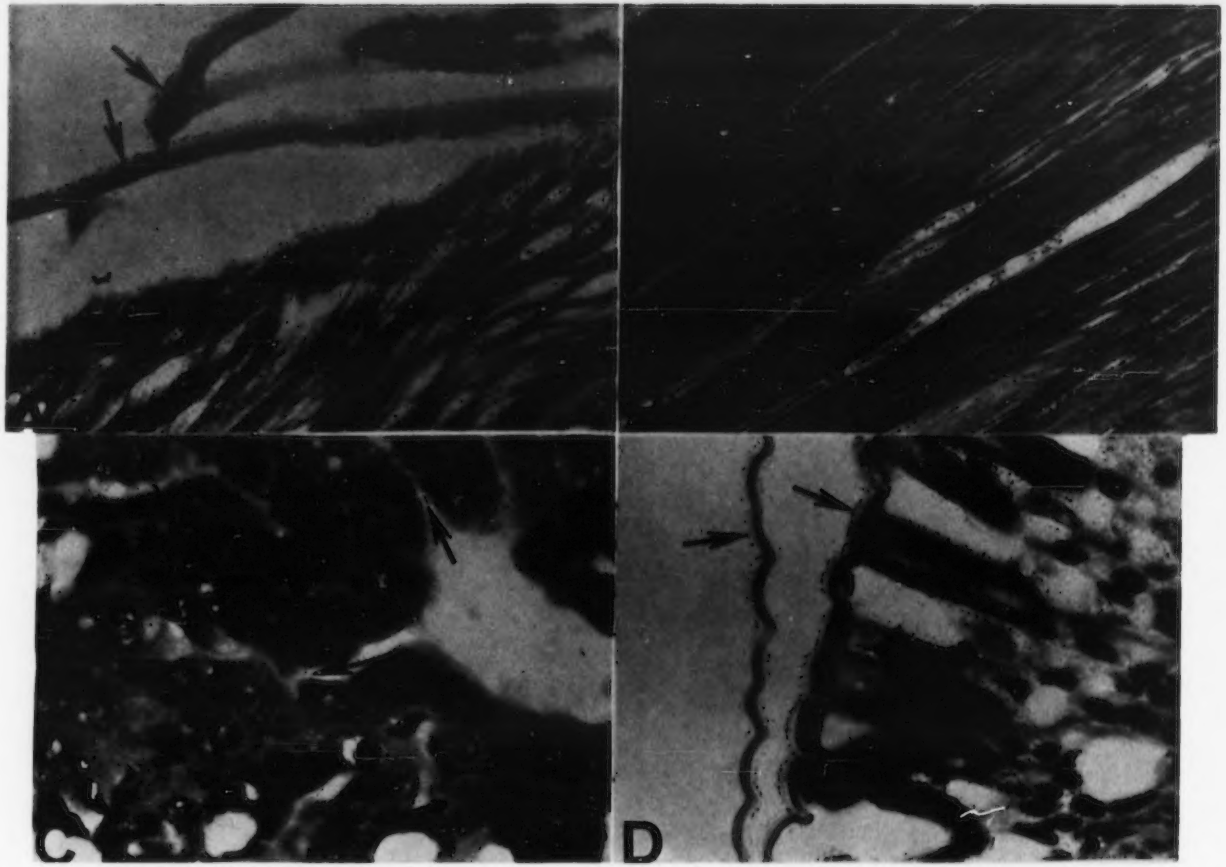

FIG. 2. Autoradiographs (400×) showing the presence of ^{65}Zn in *E. pacifica* for (A) exoskeleton, (B) muscle, (C) hepatopancreas, and (D) eye. Arrows point to areas of localization of ^{65}Zn.

diographs. We also thank Drs T. R. Rice, T. W. Duke, and D. A. Wolfe of the Bureau of Commercial Fisheries Radiobiological Laboratory, Beaufort, North Carolina, for critical review of the manuscript. This research was supported by U.S. Atomic Energy Contracts AT(45-1)1750, AT(45-1)1751, AT(45-1)1830, PHS Research Grant 5-RO1-ES00026, and PHS Training Grant 1 T1-WP-111-01.

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Mortality Among Chinook Salmon Associated with the Fungus *Dermocystidium*[1]

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ABSTRACT

Serious outbreaks of a pernicious disease caused by the fungus *Dermocystidium* are reported in both adult and juvenile salmon in the Columbia River and its tributaries. The disease evokes a characteristic histopathology and appears to cause death in a large percentage of the infected fish. The disease appears to be most virulent at water temperatures below 60 F. Some prophylactic relief is given by treatment with the organic herbicide, Diquat, at a dilution of 1:500,000 for 1 hr.

INTRODUCTION

The first record of *Dermocystidium*, a fungus parasite, in North America was the description of the species *D. salmonis* from an adult chinook salmon (*Oncorhynchus tshawytscha*) in California (Davis, 1947). Another species, *D. branchialis*, was previously reported from salmonid fishes of Europe (Dunkerley, 1914; Léger, 1914). Pauley (1967) recently observed *Dermocystidium* sp. associated with heavy prespawning mortalities of adult chinook salmon in the Priest Rapids Spawning Channel, located at mile 397 on the Columbia River, Washington (Fig. 1) and described the histopathology associated with the infections. Prior to this report, epizootics of *Dermocystidium* had not been associated with heavy mortalities among fishes in North America.

The Priest Rapids Spawning Channel was constructed as a mitigative facility for the fall chinook salmon spawning habitat inundated by Priest Rapids and Wanapum reservoirs. The Washington State Department of Fisheries operates the channel, under contract with the Public Utility District Number 1 of Grant County, Washington.

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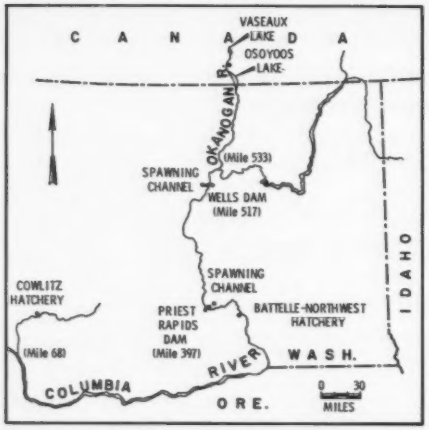

FIG. 1. Columbia River, showing localities along the river where *Dermocystidium* sp. has been observed.

Operation of the channel commenced in September 1963 and the *Dermocystidium* epidemic reported by Pauley (1967) occurred in November 1965. The prespawning mortality in 1965 totaled 1113 adult chinook, including 856 or 22.5% of the females (Table I). This compared with female prespawning mortalities of 13.6 and 5.8% in 1963 and 1964, respectively. The exact percentage of the fish infected with *Dermocystidium* in 1965 is unknown as the disease organism was not identified until after spawning commenced.

In 1966 another heavy *Dermocystidium* infection was observed among the adult salmon, beginning in early November. The prespawning mortality totaled 996 fish, including 655 or 21.8% of the females. *Dermocystidium* cysts were observed on the gills of 770 or 77.3% unspawned carcasses and 338 or 7.6% spawned carcasses recovered from the channel (Table I). Gross examinations of some unspawned carcasses also revealed the parasite in the spleen, indicating that the disease might be distributed via the circulatory system throughout the body. However, the parasite was not observed in other organs.

Dermocystidium sp. has been associated with moribund adult chinook salmon (*O. tshawytscha*) in the Priest Rapids spawning channel since the fall of 1965. Of more importance, possibly, is the fact that the disease has recently been observed in the emerging fry (*O. tshawytscha*) at Priest Rapids and in other salmon (*Oncorhynchus kisutch* and *Oncorhynchus nerka*) and in other localities in the Columbia River system.

MATERIALS AND METHODS

Tissues from 10 infected adult salmon and 10 infected fry were preserved in methanol for histological examination. Tissues stained with either hematoxylin and eosin or with Giemsa confirmed the presence of *Dermocystidium* sp. observed in fresh unstained smears of colonies taken from the gills and

TABLE I. Adult chinook prespawning mortality and the observed *Dermocystidium* infection[a] in Priest Rapids Spawning Channel, 1963–67.

Brood year	Spawning stock	Prespawning mortality						Unspawned						Spawned					
		Females		Males		Total		Females		Males		Total		Females		Males		Total	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1963	1231	98	13.6	35	6.9	10.9	–	–	–	–	–	–	–	–	–	–	–	–	–
1964	4467	100	5.8	55	2.0	155	3.5	–	–	–	–	–	–	–	–	–	–	–	–
1965	5623	856	22.5	257	14.1	1113	19.8	–[b]	–[b]	–	–	–	–	–	–	–	–	–	–
1966	5417	665	21.8	331	14.0	996	18.4	505	75.9	265	80.1	770	77.3	213	8.9	125	6.1	338	7.6
1967	3119[c]	138	6.8	45	4.1	183	5.9	28	20.3	7	15.6	35[d]	19.1	1458	77.3	542	49.2	2000	68.1

[a] *Dermocystidium* first found on the chinook in early November 1965.
[b] A high percentage of unspawned fish were infected but exact records are not available.
[c] Exclusive of 307 fish spawned artificially.
[d] Most of the other unspawned fish were found before *Dermocystidium* became visible.

spleen. The media we used to culture *Dermocystidium* from adult salmon consisted of 1/40 thioglycolate media, as described by Ray (1952, 1954), plus 5000 units of antibiotics (Penicillin and Streptomycin) in the supernate of homogenized gill tissues.

RESULTS

The histopathology observed in the gills of the adult salmon was the same as that reported previously (Pauley, 1967). The spleens exhibited a congestion and fibrosis around the *Dermocystidium* colonies, as observed by Pauley (1967).

Dermocystidium sp. cultures, taken from excised and subsequently autoclaved gill tissues of the adult salmon, developed in the thioglycolate media (Table II). Viable *Dermocystidium* organisms were first found in the thioglycolate media 3 weeks after inoculation with sterilized gill tissue and were observed until 6 weeks postinoculation. However, no *Dermocystidium* growths were observed in thioglycolate media inoculated with fresh gill tissue, which quite possibly was due to the growth of contaminants in the fresh gill tissue, which prevented the identification of *Dermocystidium*.

TABLE II. Growth of *Dermocystidium* in thioglycolate media.

Thioglycolate media additives	Thioglycolate dilutions in distilled water		
	1 ml/5 ml	2 ml/5 ml	5 ml/5 ml
1. Fresh gill tissue	–[a]	–	–
2. Autoclaved gill tissue	+[a]	+	+
3. No tissue (control)	–	–	–

[a] + is positive *Dermocystidium* growth; – is negative *Dermocystidium* growth.

Beginning in late January 1967, the cysts were found on 1966-brood chinook fry egressing from the spawning channel. This condition was not found on chinook fry during the previous year. The gross pathology of the young fish was more pronounced than in the adult salmon, in that the operculae (gill coverings) were held open by the hypertrophied gill tissues and *Dermocystidium* colonies (Fig. 2). The colonies were white and approximately the same size as those observed in adult chinooks (Fig. 3). Many of the young fish possessed *Dermocystidium* cysts externally on the anterior portion of the body, the head (Fig. 4), and occasionally on the pectoral fins. These cysts were generally located near the gills, were the infections were initially observed, but on occasion they were observed dorsally and laterally around the caudal peduncle area (Fig. 4).

Serial sections of 10 infected fry revealed a histopathology similar to that reported in adult salmon (Pauley, 1967). Additionally, cysts were also observed on the inner surface of the operculae and in the epithelium covering the isthmus. No other organs were found infected. All cysts, including those on the body surface, were surrounded by a heavy fibrosis. The *Dermocystidium* cysts and the host reaction were confined to the epithelial layers.

Routine egg and fry sampling in the spawning gravel in early 1967 showed that some fry that had not yet emerged from the gravel were infected with the disease. It appeared that the adult chinook remaining in the channel were a possible source of infection of the fry. The life cycle of *Dermocystidium* is unknown but it appeared that spores shed from the adults could have lodged in the gravel and infected the fry.

It was not possible to determine the total fry mortality caused by the disease. The fry were released into a 23-acre pond for natural rearing as they egressed from the channel. Of the 800,000 fry placed into the pond, 55% were released into the Columbia River after several months of pond rearing. This survival figure, however, is not necessarily indicative of fry loss caused by the disease, as other influencing factors such as predation and abundance or lack of natural foods contribute to the migrant survival obtained from natural rearing areas.

A chlorine treatment of the entire channel facilities was accomplished in August 1967, prior to the introduction of 1967-brood adult chinook, in an attempt to eradicate any disease-carrying spores that had become established within the spawning gravel. Despite this attempted extirpation, *Dermocystidium* cysts were again found on the adult fish. However, the prespawning mortality was greatly reduced in 1967 (Table I).

Treatments with Diquat,[3] an organic herbicide (Gilderhus, 1967), were administered to the Priest Rapids chinook in late November 1965, after the fish were heavily infected with *Dermocystidium*. These treatments were at a 1:500,000 dilution for 1 hr and appeared to be of some benefit to the adult chinook. In 1966 approximately one-half of the spawning stock was confined to the adult holding pool at the upstream end of the channel, whereas the remainder were held in the channel spawning stretches in an attempt to obtain a more uniform spawning distribution throughout the channel. The fish in the holding pool received at least two Diquat treatments per week, whereas the fish in the channel were treated with a 1:1,000,000 malachite green dye solution because of the expense of treating the entire mile-long channel with Diquat. Total prespawning mortality of the fish treated with Diquat was 7.2% as compared with 28.0% among the fish treated with malachite green (Washington Department of Fisheries, unpublished data). Diquat treatments

[3]The use of trade names in this paper does not necessarily represent an endorsement of the product. Treatment with Diquat was suggested by Richard Westgard, Washington State Department of Fisheries, because it was less expensive than salt which was suggested by Pauley (1967) as a treatment.

were immediately administered to the fish held in the channel when the prespawning mortality became excessive, but the fish were heavily infected by then. During 1967 all of the adult spawning stock received twice weekly Diquat treatments, beginning in early September, and the total prespawning mortality was only 5.9%. Even though the incidence of *Dermocystidium* was higher during 1967 among the spawned fish, it is believed that the treatments effectively controlled the disease to a point where the adult chinook could complete spawning. Therefore, Diquat appears to be an effective prophylactic treatment for this disease in adult chinook.

Pauley (1967) observed *Dermocystidium* in 1965 in several adult chinook salmon held in the hatchery at the Biology Department of the Pacific Northwest Laboratories, approximately 30 miles downstream from Priest Rapids (Fig. 1). It has subsequently been observed there in 1966 and 1967 (G. B. Pauley, unpublished data). However, there have been no apparent deaths due to the parasite.

During the fall of 1967 an apparent *Dermocystidium* epidemic occurred among the 1967 brood adult summer chinook held in the Wells Spawning Channel at Wells Dam, 120 miles upriver from Priest Rapids at river mile 517 (Fig. 1). This was the 1st year of operation at this facility. A prespawning mortality of 387 females (35.5%) occurred at this station, but it cannot be definitely stated that *Dermocystidium* sp. was the primary causative pathogen, because *Chrondococcus columnaris*, another virulent disease, was also found on the fish (Washington Department of Fisheries), unpublished data. However, Pauley (1967) has noted that *C. columnaris* was probably a secondary pathogen at Priest Rapids.

Westgard reported an outbreak of *Dermocystidium* among 1967-brood spring chinook held at the Cowlitz hatchery,[4] another Fisheries facility in its 1st year of operation. This hatchery is located on the Cowlitz River about 50 miles above its confluence with the Columbia at river mile 68 (Fig. 1).

Other occurrences of the disease were observed at the Cowlitz hatchery on the fall chinook and coho salmon (*O. kisutch*). Heavy prespawning mortalities occurred in the spring chinook, but Westgard[5] felt this was unrelated to any *Dermocystidium* infection. Virtually all of the fall chinook had heavy to moderate infections, but only a 12% prespawning mortality occurred. About 30% of the coho salmon at the station were heavily infected, but losses were insignificant, and heavily infected coho were successfully spawned.

The disease was also found by the authors during 1967 among sockeye salmon (*O. nerka*) spawning in the Okanogan River between Lakes Vaseaux and Osoyoos in central British Columbia, Canada. (Fig. 1). The Okanogan River joins the Columbia at river mile 533, 16 miles above Wells Dam. On October 11, 50 spawning sockeye were seined from the river. Nine of these were found to be infected with *Dermocystidium* cysts. All of these sockeye had either successfully spawned or were spawning at the time of capture.

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[4]Personal communication from Richard Westgard, Washington State Department of Fisheries, January 29, 1968.

FIG. 2. Chinook salmon fry heavily infected with *Dermocystidium*. Note the gill coverings held open by the hypertrophied gill tissues and the *Dermocystidium* colonies (scale in centimeters).

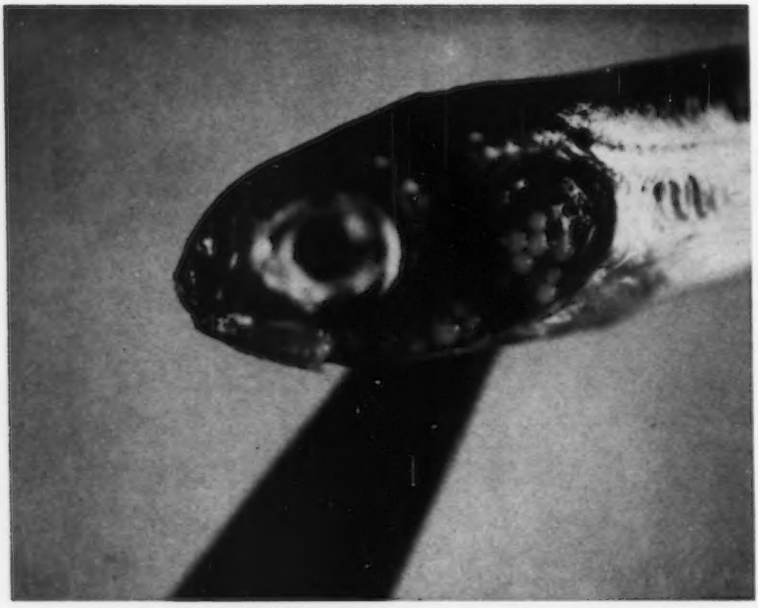

FIG. 3. Chinook salmon fry with gill cover removed to show heavy *Dermocystidium* infection in the gills.

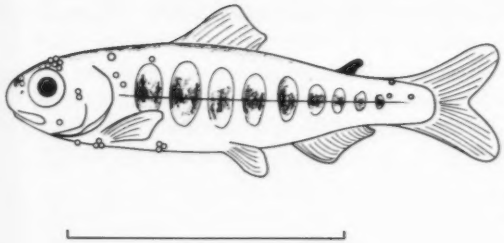

FIG. 4. Young chinook salmon showing areas of the body where *Dermocystidium* cysts were observed exclusive of the gills. Note that most of the cysts were observed anteriorly, near the gills, where the infection is initially observed. (Scale equals 1 inch.)

Unlike many other diseases of Pacific salmon, *Dermocystidium* at the Priest Rapids Spawning Channel appears to be most virulent at water temperatures below 60 F. Adult chinook are introduced into the channel beginning September 1 when the water temperature is 65 F or higher. Visible evidence of *Dermocystidium* on the fish was not found in either 1965 or 1966 until early November when the water temperature was 53–56 F. In 1967 visible evidence of *Dermocystidium* on the adult chinook was first noted in late October when the water temperature was 56 F. Infected chinook fry were found in the channel between late January and early April 1967 when the water temperature was in the range of 38–48 F. The apparent recovery from the disease of infected fry held in troughs for observation was associated with a rise in water temperature above 50 F.

The Okanogan River temperature was 56 F where the infected sockeye salmon were found. At the Wells Spawning Channel, however, visible evidence of *Dermocystidium* was found October 5, 1967 when the water temperature was 61 F. At the Cowlitz hatchery *Dermocystidium* occurred on some spring chinook in water temperatures above 60 F whereas heavily infected adult coho salmon were found in January 1968 at a water temperature of 40 F.[6]

DISCUSSION

This is not a paper of taxonomic nature, but it seems appropriate to point out that *Dermocystidium* sp. from Pacific salmon is of uncertain systematic position, although Pauley (1967) considered it a fungus. Various members of the genus *Dermocystidium* are considered Protozoa (Haplosporidia) by Reichenbach-Kline and Elkan (1965). However, *Dermocystidium* sp. is unequivocally not a Haplosporidia as it lacks a lid on the spore, which is the outstanding positive characteristic of that group (Sprague, 1963). *Dermocystidium* sp. is morphologically very similar to *Dermocystidium marinum* a fungal parasite of oysters (Ray, 1954).

It is apparent that *Dermocystidium* sp. is active through a wide range of water temperatures. However, it appears to be most virulent at water temperatures below 60 F. Undoubtedly, the physiological condition of the

[6]Personal communication from Mark DeCew, Washington State Department of Fisheries, February 6, 1968.

fish is significant in evaluating the virulence of this parasite. Water temperature does appear to be the most important environmental factor affecting the disease, because it is correlated with both initial infection in the adults and recovery in the juveniles. At present very little is known about the life history of this parasite and it is not known how the disease is transmitted. *Dermocystidium* sp. is apparently becoming increasingly widespread throughout the Columbia River system, as it has been detected with increasing frequency by the Washington State Department of Fisheries pathologists that routinely examine the Columbia River salmon for diseases.

Ray (1966a) recently tested the effect of 12 antifungal antibiotics on *D. marinum*, a lethal fungus parasite of oysters, and found that cycloheximide and streptimidone completely inhibited enlargement of *D. marinum* in thioglycollate cultures. Cycloheximide may be useful in arresting *D. marinum* in oysters held in the laboratory, because it was not toxic to oyster tissue (Ray, 1966a) and it prolonged the life of naturally infected oysters (Ray, 1966b). A similar screening test, utilizing the *Dermocystidium* sp. infecting salmon in the Columbia River, should be carried out to try to find an antifungal antibiotic that is a more satisfactory prophylactic agent than Diquat. Although some prophylatic relief is possible with Diquat, the authors believe that an extensive study of the taxonomic position, life cycle, virulence, and control of *Dermocystidium* sp. is urgently needed because of its demonstrated potential inimical effect on Pacific salmon (Pauley, 1967).

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Contribution of Protein Electrophoresis to Rockfish (Scorpaenidae) Systematics[1]

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ABSTRACT

During 1965–67, multiple hemoglobins of 1905 specimens, comprising 2 species of *Sebastolobus* and 26 of *Sebastodes*; muscle proteins of 1677 specimens, comprising 1 species of *Scorpaena*, 1 of *Scorpaenodes*, 2 of *Sebastolobus*, 2 of *Sebastes*, and 24 of *Sebastodes*; and eye lens proteins of 431 specimens, covering 1 species of *Sebastolobus* and 19 of *Sebastodes* were examined by starch-gel zone electrophoresis. *Scorpaena*, *Sebastolobus*, and *Sebastodes* specimens were collected in the eastern Pacific Ocean (California to Gulf of Alaska), and *Sebastes* specimens were collected from the western Atlantic Ocean (Newfoundland). Electropherograms were independent of sex and size. Hemoglobin electropherograms were species specific, and where variant, nongenetically linked patterns appeared, evidence suggested existence of additional species, for example, *S. diploproa* (2), *S. reedi* (2), and *S. aleutianus* (3). Genetically linked polymorphism was detected in hemoglobin protein electropherograms of *S. crameri* and muscle protein electropherograms of *S. elongatus*. Species specificity broke down with muscle proteins in many species of *Sebastodes* resulting in the separation of the 27 species examined (from this and other studies) into four distinct subgroupings. Generically distinct patterns were prominently evident in the muscle proteins of *Sebastodes*, *Sebastolobus*, *Scorpaenodes*, and *Scorpaena*, but not in *Sebastes*. The order of difference between *Sebastes* and *Sebastodes* was no more than that inherent in the four subgroupings within the latter genus. Eye lens proteins were genus-specific only. Relative value of the three groups of proteins as diagnostic tools at various levels of organization and as characters in the phylogenetic analyses of scorpaenids is discussed.

INTRODUCTION

In the northeast Pacific Ocean, from California to the Aleutian Islands, there are approximately 59 species of scorpaenids currently recorded (Phillips, 1957; Hitz, 1965; Westrheim and Tsuyuki, 1967; Strachan et al., 1968). These are assigned to four genera: *Sebastodes* (55 species), *Sebastolobus* (2), *Scorpaena* (1), and *Scorpaenodes* (1). The last three genera, and their four species, have posed no particular problems in identification. However, the genus *Sebastodes* and its numerous species continue to elude satisfactory taxonomic organization.

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Phillips (1957) reviewed the history of classifications applied to this group. Interpretations have ranged from one genus (Jordan and Evermann, 1898) to 14 genera (Jordan et al., 1930). The single-genus concept is commonly accepted by contemporary investigators, but controversy continues regarding *Sebastodes* Gill, 1861 — whether or not it should be treated as a genus congeneric with or distinct from *Sebastes* Cuvier, 1829.

Classification of species within the genus *Sebastodes* (or *Sebastes*) has proved difficult, using conventional physical morphological techniques, because so many characters have overlapping ranges among species (see Phillips, 1957, fig. 63–66). In part, the inadequacy of physical morphology data has been due to the lack of adequate numbers of specimens available for study from throughout the geographical and size ranges of each species. Such a collection would indeed require a substantial expenditure of funds and manpower.

In the scorpaenids, the need for more diagnostic characters to supplement existing ones based on comparative morphology of organized tissues has been apparent for some time. The physical properties of proteins are eminently suited to provide these characters at the molecular level as their structure is a direct translation of the genetic code of nucleic acid (reviewed by Crick, 1962, 1966; Nirenberg, 1963) and as their isolation and separation techniques are well known. Although structural analysis of proteins will reveal the most information on genetic differentiation, the methodology is as yet laborious and not adaptable for quick comparisons of large numbers of proteins on a wide scale. At the sacrifice of some genetic information, comparative electrophoretic mobilities of proteins can be used to advantage. The technique of choice currently is the high-resolution starch–gel electrophoretic approach. Certain inherent limitations in the electrophoretic analysis of proteins must be recognized. Proteins of identical mobilities are not necessarily identical in their primary structure. Within these limitations, considerable information useful in speciation can be obtained from some empirical relationships observed during the course of these studies as follows: (*a*) the protein electropherograms of any one species are virtually identical, excepting readily recognizable genetically linked polymorphisms; and (*b*) the similarities in the mobilities of proteins tend to become less so between higher levels of organization. The proteins from different tissues likewise provide useful information. For example, in fishes and in birds (Gysels, 1964), eye lens proteins have, during the course of evolution, undergone little electrophoretically detectable modification between species. Variations in electropherograms are, however, generally the rule between higher levels of organization and are useful for classifications at these taxonomic levels. Skeletal muscle proteins provide information useful in classifications at the generic, familial, and higher taxonomic levels (Tsuyuki et al., 1965; Tsuyuki and Roberts, 1966; Tsuyuki et al., 1966; Uthe et al., 1966; Tsuyuki et al., 1967) and in most cases at the species level as well. In fishes, at least, this group of proteins has been found to be perhaps the most informative towards developing a possible working method in phylogenetic

studies. Blood hemoglobins continue to be completely specific at the species and subspecies levels and are of value where conventional characters often fail. This group of proteins frequently display genetically interpretable type of polymorphisms used in gene frequency calculations in population analyses (Sick, 1961; Frydenberg et al., 1965). Examples of intraspecies polymorphisms in muscle proteins have also been encountered (Tsuyuki et al., 1965). Specific polymorphic proteins in serum as, for example, serum transferrins (Moller, 1966; Moller and Naevdal, 1966) are frequently valuable as diagnostic characters in population analyses. By virtue of their specificity, electropherograms of blood and tissue proteins show promise in the selection of biochemically uniform parental breeding stocks (Tsuyuki and Roberts, 1965) and in the diagnosis and genetic interpretations of natural and artificial hybrids.

To the authors' knowledge two electrophoretic analyses of scorpaenids have been reported: a preliminary report of the blood hemoglobins and muscle proteins of one *Sebastolobus* and eight *Sebastodes* from the Gulf of Alaska (Tsuyuki et al., 1965); and blood hemoglobin analyses of 27 species of California rockfishes (Barrett et al., 1966). The present study involves the electrophoretic analyses of 2 species of *Sebastolobus* and 26 species of *Sebastodes* from southeastern Alaska (Cape Ommaney) to Oregon; 2 species of *Sebastes* from the western Atlantic Ocean (Newfoundland); and *Scorpaena guttata* from southern California. Eight of the species in the study overlap with the study of Barrett et al. (1966).

MATERIALS AND METHODS

Source of Material

Rockfish specimens (*Sebastodes* and *Sebastolobus*) from the Oregon–southeastern Alaska region were collected aboard the *G. B. Reed* during four groundfish cruises during 1965–67 (Appendix Table I). Cruise 65-3 (August 23–September 25, 1965) investigated the distribution of Pacific Ocean perch (*S. alutus*) in selected areas from Cape Spencer, Alaska, to Cape Blanco, Oregon (Fig. 1) (Westrheim, MS, 1967). Cruise 66-2 (August 24–October 2, 1966) investigated ocean perch distribution in selected areas off southeastern Alaska and British Columbia (Westrheim, MS, 1967). Cruise 67-1 (February 1–April 24, 1967) investigated rockfish maturity off west Vancouver Island (Harling et al., MS, 1967). Cruise 67-2 (September 6–October 4, 1967) investigated the bathymetric distribution of ocean perch in south Queen Charlotte Sound and off central southeastern Alaska (Westrheim et al., 1968). All specimens were trawl-caught except *Sebastodes melanops* and *S. nebulosus* which were caught by angling along kelp beds in southeastern Alaska.

Specimens of *Scorpaena*, and *Scorpaenodes*, from southern California, were supplied by Messrs John E. Fitch and Charles H. Turner, California Department of Fish and Game. These were caught by a scuba diver; frozen shortly after capture; and shipped by air freight to the Vancouver Laboratory for processing.

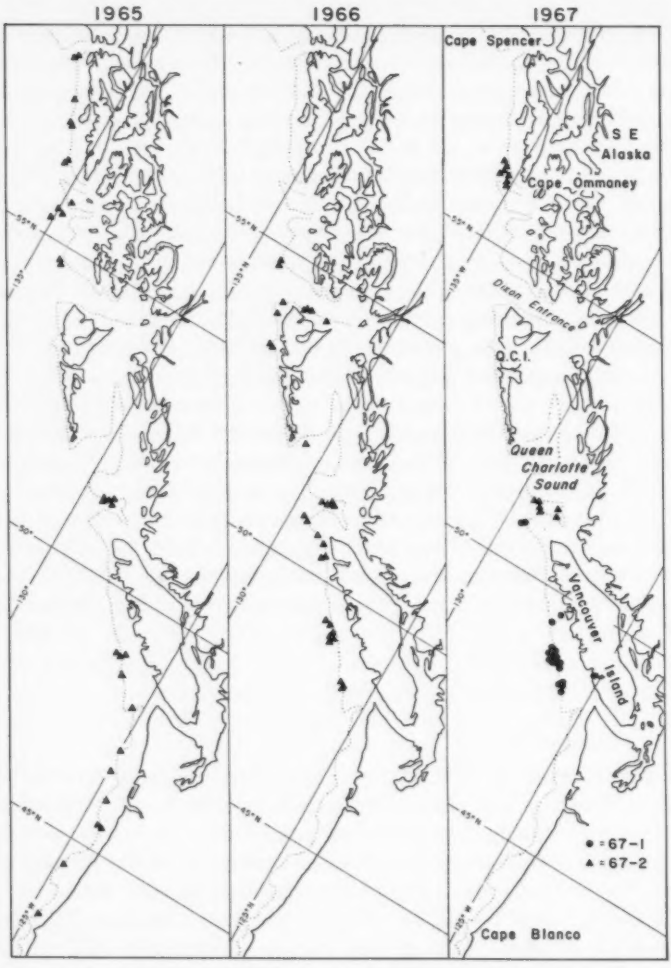

FIG. 1. Reproduction of eastern Pacific Ocean from which scorpaenids were collected during 1965–67. Solid triangles and circles represent location of hauls. Exact coordinates and depth of hauls are presented in Appendix Table I.

Specimens of *Sebastes* from the western Atlantic Ocean were provided by Dr Wilfred Templeman and Mr E. J. Sandeman, of the St. John's Biological Station (Newfoundland). These were trawl-caught; frozen at time of capture; and shipped by air freight to the Vancouver Laboratory.

PREPARATION OF PROTEIN SAMPLES FOR ELECTROPHORESIS

Within one-half hour after the fish were brought aboard the vessel, blood was withdrawn from the caudal artery into a heparinized Becton and Dickinson

4-ml-capacity vacutainer tube (No. 3274KA) fitted with a 1-inch, 22-gauge, holder-needle assembly. The whole blood was centrifuged directly in these tubes and the plasma transferred with disposable pipettes to 2-ml disposable beakers (No. B2714[2]) fitted with polyethylene caps (No. B2714) and frozen for subsequent analyses. The packed cells were hemolysed by mixing with an approximately equal volume of a distilled water suspension of Sephadex G-25, a method described by Koch et al., (1964). The suspension was centrifuged without further standing and the hemolysate separated by starch–gel zone electrophoresis by a previously described method (Tsuyuki et al., 1966) specifically adapted for operation at sea. Immediate field analyses were necessitated by the unusually poor storage qualities of most fish hemoglobins (Tsuyuki et al., 1965; Yamanaka et al., 1965). In fact, the hemoglobins of some species of rockfish deteriorate in a few hours at 0 C. The omission of the usual washing step prior to hemolysis of the erythrocytes did not result in any observable change in electrophoretic patterns with the added advantage of reducing the overall processing time of the blood sample prior to electrophoresis to $2\frac{1}{2}$ hr.

Muscle samples were likewise collected shortly after the fish were brought aboard the vessel, frozen, and stored at −20 C for later analysis at the laboratory. The muscle protein extracts were prepared as previously described (Tsuyuki et al., 1965) and separated by starch–gel zone electrophoresis in 0.023 M sodium borate buffer, *p*H 8.5, using 0.3 M sodium borate of the same *p*H in the bridge buffer solution. Electrophoresis was carried out in the same apparatus used for the separation of hemoglobins.

Biological Data on Specimens

Identification of all Pacific Ocean species was established with the assistance of artificial keys by Phillips (1957) and Hitz (1965). For the 1966 collection, fork length (nearest lower centimeter) was recorded for most specimens, and the left otolith was removed for later age assessment. For some specimens, sex was also recorded.

No validation of the age assessments was feasible due to the limited otolith collection. However, all age readings were made by two technicians at the Nanaimo Biological Station who have read several thousand otoliths from Pacific Ocean perch (*S. alutus*) and other rockfish species during the period 1963–67; hence the authors believe that the age determinations are probably reasonable.

The Atlantic Ocean specimens were identified by Mr E. J. Sandeman prior to shipment.

RESULTS

General

During 1965–67, a total of 3579 electrophoretic analyses, consisting of 1905 blood hemoglobins and 1674 muscle proteins, were completed for 31

[2]Obtained from Scientific Products, Evanston, Illinois.

species, comprising 4 genera, of scorpaenids (Table I). Table II summarizes the size composition of specimens measured in 1966. Fork lengths ranged from 20 to 76 cm for the 20 species sampled. Table III summarizes the age composition of specimens sampled in 1966. Ages ranged from 5 to 41 years. For some

TABLE I. Number of rockfish hemoglobin (H) and muscle (M) protein electropherograms examined, by species, 1965–67. (H = 1905; M = 1674.)

		1965		1966		1967		
Genus	Species[a]	H	M	H	M	H	M	Total
Sebastes	*marinus*	–	–	–	–	–	7	7
	mentella	–	–	–	–	–	3	3
Sebastodes	*aleutianus*	19	20	13	8	167	89	316
	alutus	95	431	81[b]	6	169	30	802
	aurora	–	–	–	–	2	3	5
	brevispinis	–	91	78	4	16	3	192
	caurinus	–	–	2	–	–	–	2
	ciliatus	5	5	1	1	5	–	17
	crameri	14	64	22[b]	21	98	83	302
	diploproa	14	85	19[b]	4	37	–	159
	elongatus	23	36	21	13	8	–	101
	entomelas	14	40	18	6	23	1	102
	flavidus	12	22	7	7	33	25	106
	goodei	–	–	–	–	2	–	2
	helvomaculatus	16	23	20	–	39	–	98
	jordani	–	–	6	–	2	2	10
	maliger	–	–	5	–	3	3	11
	melanops[c]	–	–	3	3	–	–	6
	nebulosus[c]	–	–	1	2	–	–	3
	paucispinis	20	50	16	–	18	–	104
	pinniger	14	23	5	2	30	22	96
	proriger	22	64	35[b]	7	47	–	175
	reedi	27	13	104[b]	44	128	–	316
	ruberrimus	8	7	3	2	7	6	33
	rubrivinctus	47	95	36[b]	4	33	–	215
	saxicola	12	53	4	4	5	3	81
	wilsoni	–	–	1	–	2	12	15
	zacentrus	22	94	47	11	25	–	199
Sebastolobus	*alascanus*	24	6	7	–	39	12	88
	altivelis	–	–	–	–	4	3	7
Scorpaena	*guttata*	–	–	–	–	–	6	6
Total:		408	1222	555	149	942	303	3579

[a]Not included are two specimens of *S. mystinus* (muscle sample) collected by angling in western Gulf of Alaska during 1964.

[b]Includes juvenile specimens.

[c]Hemoglobin electropherograms not shown as no simultaneous runs with other species were available. Caught by angling.

TABLE II. Size composition of rockfish specimens measured, by species, 1966.

Fork length (cm)[a]	Species																			
	S. aleutianus	*S. alutus*	*S. brevispinis*	*S. crameri*	*S. diploproa*	*S. elongatus*	*S. entomelas*	*S. flavidus*	*S. helvomaculatus*	*S. jordani*	*S. maliger*	*S. paucispinis*	*S. pinniger*	*S. proriger*	*S. reedi*	*S. ruberrimus*	*S. rubrivinctus*	*S. saxicola*	*S. zacentrus*	*Seb. alascanus*
20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
2	–	–	–	–	–	–	–	–	–	2	–	–	–	–	0	–	–		–	–
4	–	–	–	1	1	–	–	–	2	2	–	–	–	1	0	–	–	–	1	–
6	–	–	–	4	2	–	–	–	6	1	–	–	–	0	1	–	1	1	2	1
8	–	1	–	11	0	4	–	–	3	–	–	–	–	0	2	–	1	0	3	1
30	–	1	–	2	2	8	–	–	5	–	–	–	–	1	0	–	1	3	6	1
2	–	1	–	1	6	4	–	–	3	–	–	–	–	6	0	–	0	–	15	2
4	–	12	–	0	4	4	–	–	–	–	–	–	–	10	0	–	1	–	11	1
6	–	11	–	2	5	3	–	–	–	–	–	–	–	7	1	–	0	–	7	6
8	–	6	–	1	–	–	–	–	–	–	3	–	–	2	9	–	1	–	1	3
40	–	22	–	0	–	–	1	–	–	–	2	–	–	4	18	–	5	–	2	4
2	1	15	–	0	–	–	4	–	–	–	–	–	–	–	7	–	2	–	–	0
4	0	6	3	0	–	–	4	–	–	–	–	–	–	–	24	–	4	–	–	0
6	2	6	1	2	–	–	4	–	–	–	–	–	–	–	14	–	6	–	–	1
8	0	1	6	–	–	–	3	3	–	–	–	–	1	–	7	1	9	–	–	1
50	0	–	7	–	–	–	1	3	–	–	–	–	3	–	7	0	3	–	–	1
2	1	–	6	–	–	–	–	1	–	–	–	–	1	–	3	0	0	–	–	–
4	0	–	7	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–
6	1	–	3	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
8	0	–	3	–	–	–	–	–	–	–	–	2	–	–	–	0	–	–	–	–
60	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	0	–	–	–	–
2	0	–	–	–	–	–	–	–	–	–	–	5	–	–	–	0	–	–	–	–
4	1	–	–	–	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–
6	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
70	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–
4	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–
6	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Total	7	82	36	24	20	23	17	7	19	5	5	15	5	31	94	3	35	4	48	22

[a]Measured to nearest lower centimeter and grouped into 2-cm intervals.

specimens, lengths were not recorded for all specimens from which otoliths were collected.

HEMOGLOBIN ELECTROPHEROGRAMS

Of the various groups of fish proteins investigated, blood hemoglobin electropherograms have been found to be the most useful diagnostically at

TABLE III. Age composition of rockfish from which otoliths were collected in 1966.

Age (*years*)	*S. aleutianus*	*S. alutus*	*S. brevispinis*	*S crameri*	*S. diploproa*	*S. elongatus*	*S. entomelas*	*S. flavidus*	*S. helvomaculatus*	*S. jordani*	*S. maliger*	*S. paucispinis*	*S. pinniger*	*S. proriger*	*S. reedi*	*S. ruberrimus*	*S. rubrivinctus*	*S. saxicola*	*S. zacentus*	*Seb. alascanus*
5	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
6	–	0	–	0	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–
7	–	0	–	4	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–
8	–	0	–	9	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4	–
9	–	1	–	4	–	–	–	–	–	–	–	–	–	2	2	–	–	–	0	–
10	–	2	–	0	–	–	–	–	–	1	–	–	–	1	0	–	1	–	0	–
1	–	2	–	0	1	–	–	–	–	1	–	–	–	2	1	–	1	–	3	–
2	–	1	1	0	0	–	1	–	–	3	–	–	–	6	3	–	1	–	3	2
3	–	13	0	3	2	1	2	1	–	–	–	2	–	6	10	–	1	1	5	0
4	–	13	1	1	0	3	2	1	3	–	–	1	–	3	15	–	1	0	8	1
15	–	11	5	0	0	2	3	0	2	–	–	1	–	2	7	–	2	0	6	3
6	2	8	4	0	0	3	0	2	0	–	–	1	–	4	10	–	1	0	9	0
7	0	10	2	0	0	3	0	1	2	–	–	1	–	4	11	–	1	0	4	3
8	0	7	4	0	2	4	5	1	0	–	–	1	–	1	5	–	5	0	3	4
9	0	3	4	0	3	3	1	1	1	–	2	2	–	–	5	–	3	1	1	6
20	2	6	5	0	6	1	1	–	1	–	0	2	–	–	4	–	6	2	0	2
1	0	7	3	0	2	1	1	–	2	–	0	0	–	–	2	–	3	–	1	1
2	0	0	2	0	3	2	0	–	1	–	1	1	1	–	6	1	2	–	0	1
3	0	2	0	0	1	–	0	–	0	–	0	2	1	–	2	0	1	–	0	1
4	0	1	1	0	–	–	0	–	2	–	1	2	0	–	2	0	4	–	0	0
25	0	1	1	0	–	–	0	–	1	–	0	–	0	–	1	0	2	–	1	3
6	0	1	1	1	–	–	1	–	2	–	0	–	2	–	3	0	3	–	–	0
7	1	–	3	0	–	–	–	–	0	–	0	–	1	–	0	0	0	–	–	0
8	0	–	1	1	–	–	–	–	0	–	1	–	–	–	1	0	1	–	–	0
9	0	–	–	–	–	–	–	–	0	–	–	–	–	–	1	1	0	–	–	1
30	0	–	–	–	–	–	–	–	0	–	–	–	–	–	0	0	0	–	–	–
1	1	–	–	–	–	–	–	–	1	–	–	–	–	–	2	0	0	–	–	–
2	0	–	–	–	–	–	–	–	1	–	–	–	–	–	–	0	1	–	–	–
3	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
4	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
35	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
6	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
7	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
8	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
9	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	7	90	38	24	20	23	17	7	19	5	5	16	5	31	95	3	40	4	48	28

the species level. In over 125 species examined, no two identical patterns have been encountered. However, there are certain disadvantages associated with the use of these proteins for the above purposes. Firstly, hemoglobins may undergo ontogenetic changes. This phenomenon has been observed for *Salmo salar* (Koch et al., 1964) and for *Oncorhynchus* (Vanstone et al., 1964) during parr–smolt transformation. No such phenomenon has yet been noted for scorpaenids. Benthic-dwelling juvenile specimens of *S. alutus*, *S. crameri*, *S. diploproa*, *S. proriger*, *S. reedi*, and *S. rubrivinctus* possessed the same patterns as adult fish. It seems likely that ontogenetic changes, if present, occur during the pelagic–benthic transformation phase of the life history. Secondly, and more disconcertingly, the electrophoretic mobility characteristics of blood hemoglobins of the rockfishes examined so far were found to undergo changes during storage at 4 C, and in many species about 4 hr after preparation for electrophoresis. Part, but not all, of this change has been reported to be associated with the oxidation of the iron to the ferric state of methemoglobin (Yamanaka et al., 1965). If the highly specific multiple hemoglobin electropherograms are to be used for species identification, conditions must be selected for reproducibility of patterns. In our first such study of rockfishes (Tsuyuki et al., 1965) delay in air shipment of blood samples from Alaska to laboratories in Vancouver where electrophoretic analyses were carried out resulted in indistinct patterns for many species. Although stabilizing procedures involving derivitization of oxyhemoglobins to carbomonoxy — or cyanomet — forms have been employed for hemoglobins from other sources of fishes, these methods were not conveniently adaptable to analyses of large numbers of samples under difficult field conditions and were largely the determinant factor in the decision to base all our comparative electropherograms on mobility characteristics of oxyhemoglobins. For this end, electrophoretic apparatus was modified (Tsuyuki et al., 1966) to enable convenient operations at sea where the blood could be withdrawn immediately and analyzed as quickly as possible. With rockfishes, the speed of operation is important, as fish are trawl-caught from depths reaching 200 or 300 fath, and are dead or dying when brought aboard the vessel. Furthermore, only fishing operations of this type can readily produce the quantities of fish required for simultaneous comparisons of large numbers of rockfishes.

The hemoglobin electropherograms of 2 species of *Sebastolobus* and 24 species of *Sebastodes* are shown in Fig. 2. The patterns are not arranged in the order of increasing concavity of the interorbital area after the review of Phillips (1957), but grouped simply by a combination of similarities in muscle as well as hemoglobin patterns. The schematic presentation of electropherograms resulted in part from certain limitations in electrophoretic analyses carried out on vessels under constant motion. The first of these precluded the use of wide gel strips for simultaneous comparisons of large numbers of samples. Difficulties encountered in the pouring of the gels, as well as the standard width of commercially available stainless steel razor blades, limited the gel width to 1½ inches. Secondly, the bridge buffer solutions were placed in narrow

(1¾ inches) compartments to avoid spillage under motion. The narrow gels resulted in the inevitable slight mobility differences between gel strips encountered in zone electrophoresis. Undoubtedly, a more elaborate apparatus can be devised at far greater cost and sacrifice of simplicity. Sampling procedures also impose limitations, for little control can be exercised over the species caught in any one trawl. To circumvent these difficulties, at one time or another during the 3-year program, the electropherogram of the most widely distributed species in these waters, *S. alutus*, was placed adjacent to those of all other species in this study. In this way the patterns of all species were schematized relative to *S. alutus* initially and later cross-checked against any other species which happened to be placed next to each other. In addition, the hemoglobin solutions of every species were analyzed immediately, and after 4–24 hr storage, to determine the changes introduced in patterns. These changes are also schematized in Fig. 2. Storage experiments were often unintentional due to occasional storms postponing electrophoretic analyses until sheltered waters were reached. Representative patterns specific for each species are typical patterns observed over a period of 3 years. The actual electropherogram from which the patterns are schematized are also shown in Fig. 2. With the exception of *S. aleutianus*, *S. crameri*, *S. diploproa*, and *S. reedi*, the 24 *Sebastodes* and 2 *Sebastolobus* in this study possessed species-specific hemoglobin electropherograms. Those species displaying more than one pattern are discussed below.

Sebastodes aleutianus. — Four hemoglobin patterns, tentatively labelled A, B, C, and D, were obtained from this species (Fig. 2, Table IV). Storage studies conducted on all four types indicated little change. Patterns A, B, and C were deemed unrelated, and D was considered a rare hybrid pattern of A and B. No D type was encountered among 32 specimens collected during 1965–66, and only 3 were observed among 167 specimens in 1967. Based on the 1966 data, no relationship was evident between patterns A, B, or D sex, length (42–64 cm), or age (16–41 years). Although no fish with pattern C were measured or aged, none were less than 70 cm (fork length) and their average weight was approximately 30 lb, as opposed to 5–10 lb for A, B, and D fish. Some relationship of pattern type to area and depth was evident. Pattern A fish were most prevalent (81 of 123 sampled) in the Queen Charlotte Sound and Vancouver Island areas virtually throughout the depth range fished (92–240 fath). Pattern B fish were most common (37 of 62 sampled) in the southeastern Alaska area, and they also exhibited no apparent relationship with depth. Pattern C fish were encountered only at depths exceeding 180 fath and usually predominated over the other pattern types at these depths.

Sebastodes crameri. — Genetic polymorphism was evident in hemoglobin patterns designated A, B, and AB (Fig. 2). This is the only rockfish species studied, except possibly *S. eos* (Barrett et al., 1966), whose hemoglobins display this type of polymorphism. The frequency of occurrence of the pattern types by haul, area, and depth are shown in Table V. Gene frequency calculations are not shown here as sampling from the various areas was insufficient. Based on the 1966 data, no relationship was evident between pattern types A, B, and

TABLE IV. Numbers of *S. aleutianus* hemoglobin electropherograms examined by haul, by polymorphic pattern, 1965–67.

Haul no.	Depth (*fath*)	Pattern A	B	C	D
	Southeastern Alaska (Sept.)				
67-2-39	153–156	–	3	–	–
67-2-34[a]	158–166	–	18	–	1
65-3-15	140–180	1	2	–	–
65-3-38	122–200	–	1	–	–
67-2-31	200–202	–	4	6	–
65-3-26	142–214	–	–	5	–
67-2-33	216–218	2	4	10	–
67-2-40	218–219	–	5	–	–
Subtotal		3	37	21	1
	NW Queen Charlotte Island (Sept.)				
66-2-29	196–200	0	0	5	0
	S Queen Charlotte Sound (Aug.–Sept)				
66-2-14	92–112	1	–	–	–
67-2-9	127	–	4	–	–
65-3-5	144–150	1	–	–	–
66-2-9	148–151	7	–	–	–
67-2-17	152–154	17	–	–	–
67-2-21	154	5	–	–	–
Subtotal		31	4	0	0
	SW Vancouver Island (Feb.–Apr.)				
67-1-51	150	1	–	–	–
-35	168–176	2	–	–	–
-14	170–188	3	–	–	–
-3	142–194	1	–	–	–
-42	180–196	1	–	–	–
-53	192–198	18	1	–	1
-1	194–198	–	–	2	–
-25	182–202	2	–	2	–
-37	198–208	1	–	1	–
-68	205–210	–	–	1	1
-55	205–214	8	–	–	–
-38	220–226	1	6	4	–
-27	222–240	9	6	2	–
-85	230–240	3	1	1	–
-40	286–300	–	–	9	–
Subtotal		50	14	22	2
Grand total		84	55	48	3

[a]One specimen not included which possessed an "odd" pattern resembling B.

TABLE V. Numbers of *S. crameri* hemoglobin electropherograms examined by area, haul, depth, and pattern, 1965–67.

Haul no.	Depth (*fath*)	Pattern A	Pattern B	Pattern AB
	SE Alaska			
65-3-9	160–164	0	0	1
	S Queen Charlotte Sound			
67-2-17	–	1	–	1
	SW Vancouver Island			
66-2-54	112–116	7	3	6
66-2-47	122	0	0	1
66-2-51	178–180	1	1	3
67-1-34	159–164	0	0	2
-24	160–172	3	0	1
-35	168–176	6	1	2
-14	170–180	10	2	5
-23	181–184	5	0	4
-3	142–194	0	1	1
-42	180–196	3	0	1
-1	194–198	0	0	1
-25	182–202	6	1	2
-37	198–208	9	3	4
-55	205–214	1	2	6
-38	220–226	0	0	1
-27	222–240	1	0	1
-15	230–240	2	0	4
-21	150–278	0	0	1
Subtotal		54	14	46
	Washington			
65-3-61	116–126	2	1	1
	Oregon			
65-3-74	90–92	3	0	2
65-3-69	128–134	2	0	2
Subtotal		5	0	4
Grand total		61	15	50

AB, and sex, size (24–46 cm), or age (5–28 years) of specimens. Likewise, for the 1965–67 data, there were no apparent relationships between pattern types and area or depth of capture. However, the sampling was too limited for adequate appraisal.

Sebastodes diploproa. — This species also exhibited more than one hemoglobin electropherogram (Fig. 2). Pattern A appears to be the most common, and C represents a storage change of A. Pattern B, of which 13 were observed

out of 72 specimens analysed over the 3-year period, definitely appears to be a variant type occurring not uncommonly. Based on the 1966 data, no relationship was evident between pattern types and sex, size (24–36 cm), and age (11–23 years) of specimens. Likewise, for the 1965–67 data, no relationship was apparent between pattern types and area or depth of capture (Table VI). However, sampling was again too limited for adequate appraisal.

TABLE VI. Numbers of *S. diploproa* hemoglobin electropherograms examined by area, haul, depth, and pattern, 1965–67.

Haul no.	Depth (*fath*)	Pattern A	Pattern B	Pattern C[a]
	SE Alaska			
65-31-3	120–140	1	0	0
	S Queen Charlotte Sound			
67-2-21	–	12	4	0
	SW Vancouver Island			
66-2-54	112–116	3	2	–
66-2-47	122	2	1	1
66-2-48	127–136	3	1	1
65-3-43	156–160	4	–	2
66-2-51	178–180	3	–	2
67-1-51	150	1	–	–
-4	132–152	1	–	–
-34	159–164	1	2	–
-24	160–172	–	–	1
-3	142–194	2	–	–
-42	180–196	2	1	1
-21	150–278	10	–	–
Subtotal		32	7	8
	Washington			
65-3-58	108–158	1	0	0
	Oregon			
65-3-78	128–130	2	1	–
65-3-69	128–134	1	1	2
Subtotal		3	2	2
Grand total		49	13	10

[a]Represents storage change of A.

Sebastodes reedi. — Details of the type A and B hemoglobin electropherograms of this new species have been reported elsewhere (Westrheim and Tsuyuki, 1967). Type A fish predominated (75–93%) in the three areas off British Columbia where substantial aggregation of *S. reedi* were discovered

and sampled. No morphometric or meristic differences have been detected yet between type A and B fish.

The hemoglobin electropherograms of *S. caurinus*, *S. ciliatus*, *S. wilsoni*, *S. aurora*, and *Sebastolobus altivelis*, are based on six or less specimens and could well reveal variant patterns upon further sampling.

Muscle Electropherograms

Electropherograms of muscle proteins are shown for 24 species of *Sebastodes* (Fig. 3). These are representative patterns from 1674 specimens analyzed over 3 years (Table I). As a reference standard, *S. alutus* is included in every starch gel strip. *Sebastodes maliger*, *S. jordani*, *S. aurora*, and *S. wilsoni* are shown adjacent to *S. pinniger*, *S. flavidus*, *S. alutus*, and *S. aleutianus*, respectively. The pattern of juvenile *S. alutus* is included to show that it is no different from the adult. Sample sizes were kept large enough to allow for chance encounter of polymorphic patterns, except for *S. melanops*, *S. maliger*, *S. nebulosus*, *S. jordani*, and *S. aurora* in which six or less specimens were available. In one species, *S. alutus*, 457 specimens collected from the Gulf of Alaska to Oregon were analyzed. Among species numbering more than six specimens, only two instances of polymorphism in muscle protein patterns demonstrable by electrophoresis were encountered. One was the genetically linked polymorphism in *S. elongatus*, and the other, the odd muscle pattern in *S. crameri* of which 2 were observed in 64 specimens in 1965, 1 out of 21 in 1966, and 5 out of 83 in 1967. In the 1966 and 1967 collections, four of the odd muscle patterns corresponded to the AB hemoglobin patterns and two with the A pattern. The occurrence of the odd pattern with the AB type hemoglobin implies its presence in the B type, though this was not actually observed. It is also emphasized here that *S. aleutianus*, *S. diploproa*, and *S. reedi*, which show more than one hemoglobin pattern unexplainable by genetic polymorphism, have only one muscle pattern.

Eye Lens Electropherograms

Eye lens proteins of 431 specimens from the 1965 collection covering 19 *Sebastodes* and 1 *Sebastolobus* indicated specificity at the generic level only. Minor differences found in the *Sebastodes* species were variable and of little value as diagnostic tools at the species level. In this connection the lens proteins appear to be of even less value diagnostically than muscle proteins, and in species other than rockfishes do not distinguish, for example, four species of *Oncorhynchus* whereas muscle proteins are completely specific (Tsuyuki and Roberts, 1966).

DISCUSSION

A comparison of the electropherograms of blood and tissue proteins of a large number of species with existing taxonomic classification has revealed a remarkable parallelism between similarities of electrophoretic patterns of

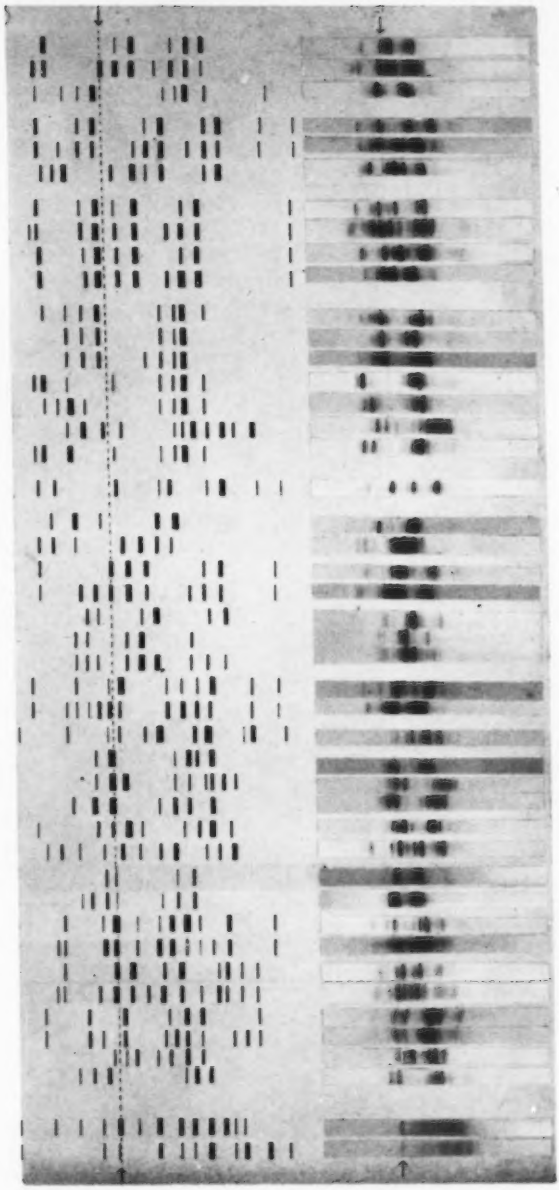

FIG. 2. Starch-gel electropherograms of scorpaenid hemoglobins. The mobility of protein zones of each species are schematized and corrected relative to *S. alutus* used as reference standard. The uncorrected photographic reproduction of the patterns are also presented. The arrows indicate points of sample application. In this and subsequent figures, the anode is to the right and the cathode to the left.

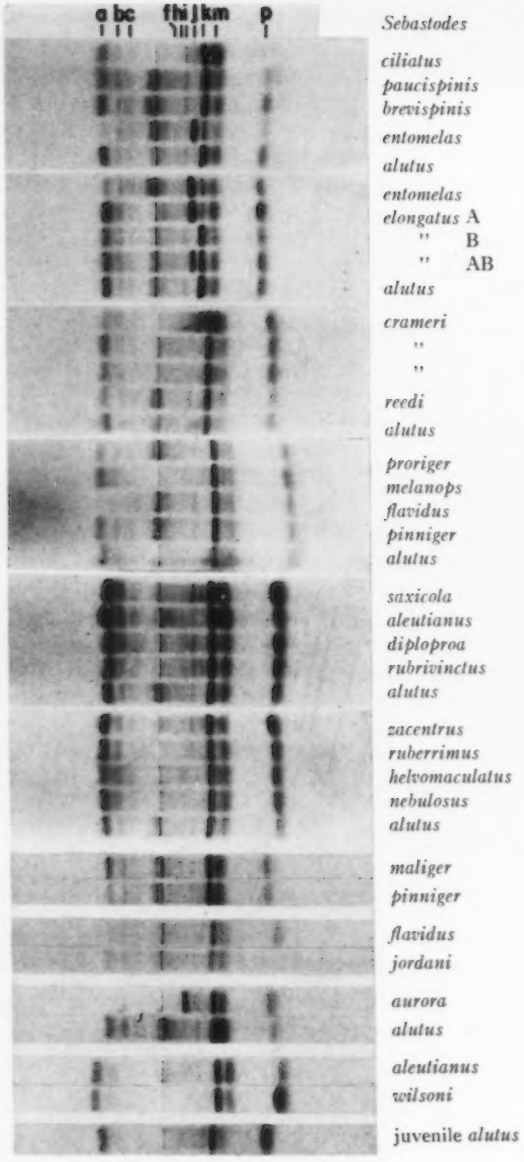

FIG. 3. Starch-gel electropherograms of muscle proteins of *Sebastodes*. The pattern of *S. alutus* is included frequently as reference standard.

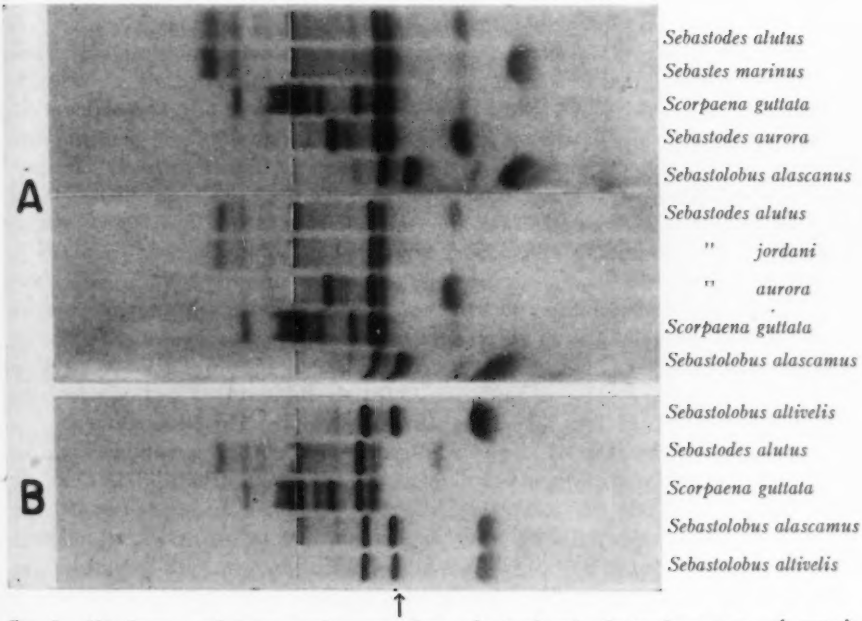

FIG. 4. (A) Inter- and intrageneric comparison of starch-gel electropherograms of muscle proteins of scorpaenids. (B) Comparison of muscle proteins of two species of *Sebastolobus* with *Sebastodes* and *Scorpaena*.

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closely related species and their phylogenetic relationships established through consideration of osteological and other characters. Thus if two species are closely related phylogenetically their electropherograms were generally found to be similar or identical within the limits of specificity of the particular group of proteins under consideration. At the species level, identity in electropherograms between two or more species, as are often found in muscle and eye lens proteins, reflects limitations in the electrophoretic approach as a method of detecting genetic differences expressed in proteins. At this level, also, one or more proteins with the same mobility would in all likelihood show differences in primary structure. Differences not detectable by electrophoresis of the whole protein could result readily by substitutions in the polypeptide chain of hydrophobic by hydrophobic amino acids, or of hydrophilic by hydrophilic amino acids of the same charge (Epstein, 1964, 1966). Even in randomly interbreeding populations of a single species, genetically linked protein polymorphisms, involving interchange of the above type, would not be detected by this method. That such substitutions, though not yet demonstrated conclusively in fishes, must occur in many species, follows as a logical extension of the numerous observations of electrophoretically detectable type of interchange within the protein molecule. The interpretation of electropherograms in the following discussion must of necessity be considered within these limitations. It should also be emphasized that this study is by no means a complete analysis of all scorpaenid species in the eastern Pacific Ocean, nor even of all species reported to exist off British Columbia.

The observed hemoglobin patterns, A, B, C, and D, for fishes keying to *S. aleutianus* reveal certain points of interest. In pattern types A and B, common mobilities of all anodic hemoglobin zones indicate a close relationship may have existed at some earlier evolutionary era, but the difference in the cathodic zones point to the absence of gene flow between currently living populations of the two groups. Pattern D appears to be a chance hybrid between A and B and its infrequent occurrence, 3 out of 200, suggests the existence of some isolation mechanism between A and B. Notably, pattern A predominated over B in the Vancouver Island (50 to 14) and Queen Charlotte Sound (31 to 4) areas, and dominance reversed (3 to 37) in the Southeastern Alaska area.

Where two polymorphic patterns were encountered in any single interbreeding species, the hybrid type hemoglobin patterns are quite common, as, for example, in *S. crameri* (Table V) in this study and in *Gadus morhua* (Sick, 1961) in the Atlantic Ocean. Pattern C of *S. aleutianus* does not appear to have much in common with either A or B and was found only in exceptionally large fish, which in turn were only caught in deep water. On the basis of electrophoretic data, it is suggested that the *S. aleutianus* complex is comprised of at least two separate species. Further investigations are under way.

For the 72 specimens of *S. diploproa*, not a single hybrid pattern of A and B was observed — pattern C resulted from storage changes. Furthermore, no variations on these two patterns were found. Sexual dimorphism was not

indicated. The total absence of the hybrid form pattern raises the possibility that more than one distinct group may exist in *Sebastodes* keying to *S. diploproa* sampled in the areas covered. This species is under further investigation.

A general consideration of the muscle protein patterns of the 24 species of *Sebastodes* shown in Fig. 3 brings out several points of interest. Firstly, many species display identical or near identical patterns. Secondly, the muscle protein patterns of the species in this genus fall into four distinct groups (Table VII). No particular significance is as yet attached to the order in which these groups are considered. Group 1 is characterized by the deletion of a major protein zone migrating most anodally. In this category belong *S. ciliatus* and *S. jordani* shown in Fig. 3, *S. polyspinis* from a previous report (Tsuyuki et al., 1965), and *S. mystinus* from a 1964 collection (inshore angling, Shumagin

TABLE VII. Grouping of 27 species of *Sebastodes* based on muscle protein and subgrouping based on hemoglobin electropherograms.

Group	Species	Zonal patterns
1	*ciliatus* *jordani* *mystinus* *polyspinis*	*Polyspinis* and *ciliatus* have very closely related pattern.
2	*elongatus* *entomelas*	Several zones of common mobility shared.
3	*aurora*	
4	*flavidus* *melanops* *pinniger*	Somewhat the same distribution of zones. The slightly greater cathodal mobility of the most cathodic zone of *flavidus* is the only difference between this species and *pinniger*..
	aleutianus[a] *alutus* *zacentrus*	Anodal zones of *aleutianus* identical to *alutus*. *Alutus* and *zacentrus* have many zones of identical mobilities.
	caurinus *nebulosus*	Somewhat similar zoning patterm
	aleutianus[b] *brevispinis* *crameri* *diploproa* *helvomaculatus* *maliger* *paucispinis* *proriger* *reedi* *ruberrimus* *rubrivinctus* *saxicola* *wilsoni*	No particular relationship observed in these 12 species.

[a]Refers only to *aleutianus* pattern types A, B, and D.
[b]*Aleutianus* pattern type C.

Islands) not reported before. Group 2 is characterized by the addition, indicated by an arrow, of a major protein as in *S. elongatus* and *S. entomelas*. One of the polymorphic patterns (A) of the former is nearly identical to the latter. Although the B pattern of *S. elongatus* is like that of *S. alutus* it is not placed in group 4 below since this is clearly an instance of genetically linked polymorphism belonging to the same interbreeding population involving pattern types A, B, and AB. Group 3, represented by a single species, *S. aurora*, displays a pattern related to, but greatly different from, the remainder, suggesting differences at the generic level. Group 4, consisting of the remaining 20 species studied, have identical or near identical patterns, indicating that an exceptionally close genetic relationship exists with respect to muscle proteins. To facilitate discussion, this group is placed in a central role around which subgroupings based on addition or deletion of protein zones are compared. This group also demonstrates the highly specific nature of hemoglobin patterns compared with the muscle protein patterns. These 20 species of *Sebastodes*, along with 2 species of catostomids (Tsuyuki et al., 1967) provide the only examples so far encountered of deviation from species specificity of muscle protein patterns demonstrable by electrophoresis. It is expected that more such examples will be found upon investigation of other species. On the other hand, it also indicates that the muscle protein patterns can be used advantageously to diagnose the more drastic phylogenetic differences facilitating the grouping of fishes at the generic and subgeneric levels. Further breakdown of these groupings can then be accomplished with the highly specific hemoglobins.

When the hemoglobins and muscle patterns are considered together, further interesting relationships become evident (Table VII). In group 1, *S. polyspinis* and *S. ciliatus* (Tsuyuki et al., 1965) have similar hemoglobin patterns which are different from that of *S. jordani*. Hemoglobin patterns of *S. mystinus* were not available. In group 2, the similarity between the hemoglobin patterns of *S. entomelas* and *S. elongatus* on the anode side is not coincidental. In group 3, *S. aurora* displays a pattern quite different from all the rest. The hemoglobin patterns of the remaining species of group 4 vary greatly, but certain subgroupings are apparent. *Sebastodes melanops*, *S. flavidus*, and *S. pinniger* show similar patterns. This observation was also shown for California specimens of the first two species by Barrett et al. (1966). *Sebastodes alutus*, *S. aleutianus* (A, B, and D), and *S. zacentrus* have similar patterns. The anodic hemoglobins of *S. alutus* and the A, B, and D patterns of *S. aleutianus* are identical, and *S. zacentrus* is strikingly like *S. alutus*. The similarity of *S. caurinus* (Fig. 2) and *S. nebulosus* (not shown) from California waters is also found in specimens from northern waters. Hemoglobin patterns of *S. nebulosus* and *S. melanops* are not shown here because these were not compared adjacently to any of the other species to obtain relative mobilities. The remaining 12 species (and type C *S. aleutianus*) of group 4 have widely different hemoglobin patterns and have been treated together as one group until further evidence becomes available. The above groupings have been

formulated independently of any morphological or osteological considerations, are based strictly on information that can be derived from protein electropherograms established from a study of over 125 species of marine and freshwater fishes, and are subject to change pending further investigation. A full evaluation of phylogenetic relationships should take into consideration all possible criteria useful for these purposes.

Although hemoglobin electropherograms are extremely useful as a diagnostic tool in species identification and intraspecies genetic variations, they are more difficult to interpret phylogenetically. The very high degree of specificity often emphasizes differences as well as similarities. Comparative electropherograms from previous studies have indicated that more differences often exist between two very closely related than distantly related species. However, it has been observed repeatedly that closely related species share many protein zones of the same electrophoretic mobilities and, when their electropherograms are used in conjunction with the broader groupings by muscle protein electropherograms, provide characters for further subgroupings. An examination of the comparative electropherograms in Fig. 2 will quickly point out the confusion that would follow any attempt to establish generic or intrageneric breakdown of the rockfishes on the basis of hemoglobin alone. The very low degree of specificity of lens proteins at the species levels, and less frequently at the generic levels, could conceivably be used to advantage in systematics at the higher orders of classification, comparable in usefulness to double stranded nucleic acid recombination studies (Hoyer et al., 1964).

If previous results linking similarities in muscle protein electropherograms with phylogentic relationships so far observed in the families Salmonidae (Tsuyuki and Roberts, 1966; Tsuyuki et al., 1966), Catostomidae (Tsuyuki et al., 1967), Esocidae, Centrarchidae, Percidae, and Petromyzontidae (Uthe et al., 1966), and other groups, are meaningful, this parallelism could well be a general phenomenon which may be used to advantage. In the family Scorpaenidae the relationships by muscle protein electropherograms are again demonstrable (Fig. 4A) and largely reflect currently recognized generic segregation with some exceptions. Furthermore, these sets of characters provide additional useful information difficult to realize by existing approaches. Both species of *Sebastes*, *marinus* and *mentella* (not shown), have almost identical patterns. *Sebastolobus alascanus* and *S. altivelis* have nearly identical patterns, except for the slight difference in the mobility of anodic zone indicated by an arrow (Fig. 4B). All six specimens of *Scorpaena guttata* analyse to a single pattern as do all three specimens of *S. aurora*. The patterns of group 1 *Sebastodes*, represented by *S. jordani*, *S. mystinus*, *S. polyspinis*, and *S. ciliatus*, and group 2, represented by *S. elongatus* and *S. entomelas*, and both species of *Sebastes* differ from each other and from the large group 4 of *Sebastodes*, either by a deletion or addition of a single major protein zone. On the basis of muscle proteins, therefore, the order of difference between the genera *Sebastes* and *Sebastodes* is no greater than between groups 1, 2, and 4 of the latter genus. Electrophoretic evidence does not support the sep-

aration of the two genera based on morphological characters. It must be emphasized, however, that the chemical criteria for distinguishing segregations at the species and generic levels are still ill-defined and the most that can be

TABLE VIII. Summary of muscle protein patterns of 25 species of *Sebastodes*.

Species	Maximum no. of muscle protein zones in *Sebastodes*[a]										Comparison with group 4 *Sebastodes*		
												Type of difference	
	a	*b*	*c*	*f*	*h*	*i*	*j*	*k*	*m*	*p*	No. of common zones	Addition of zones	Deletion of zones
Group 4													
aleutianus	+	+	+	−	−	+	−	+	+	+	7		
alutus	+	+	+	−	−	+	−	+	+	+	7		
brevispinis	+	+	+	−	−	+	−	+	+	+	7		
caurinus	+	+	+	−	−	+	−	+	+	+	7		
crameri	+	+	+	−	−	+	−	+	+	+	7		
diploproa	+	+	+	−	−	+	−	+	+	+	7		
flavidus	+	+	+	−	−	+	−	+	+	+	7		
helvomaculatus	+	+	+	−	−	+	−	+	+	+	7		
maliger	+	+	+	−	−	+	−	+	+	+	7		
melanops	+	+	+	−	−	+	−	+	+	+	7		
nebulosus	+	+	+	−	−	+	−	+	+	+	7		
paucispinis	+	+	+	−	−	+	−	+	+	+	7		
pinniger	+	+	+	−	−	+	−	+	+	+	7		
proriger	+	+	+	−	−	+	−	+	+	+	7		
reedi	+	+	+	−	−	+	−	+	+	+	7		
ruberrimus	+	+	+	−	−	+	−	+	+	+	7		
rubrivinctus	+	+	+	−	−	+	−	+	+	+	7		
saxicola	+	+	+	−	−	+	−	+	+	+	7		
wilsoni	+	+	+	−	−	+	−	+	+	+	7		
zacentrus	+	+	+	−	−	+	−	+	+	+	7		
Group 2													
elongatus (AB)	+	+	+	−	−	−	+	+	+	+	6	1	1
entomelas	+	+	+	−	−	−	+	+	+	+	6	1	1
Group 1													
ciliatus	+	+	+	−	−	+	−	+	+	−	6		1
jordani	+	+	+	−	−	+	−	+	+	−	6		1
Group 3													
aurora	−	−	−	+	+	−	−	+	+	+	3	2	4

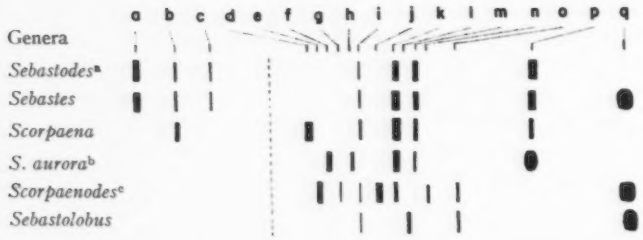
[a]Letters *a*, *b*, *c*, *f*, *h*, *i*, *j*, *k*, *m*, and *p* represent from cathode to anode, clearly defined and consistently occurring minor and major protein zones in the genus *Sebastodes* studied. The zones are lettered to correspond with those shown in the intergeneric comparison of Table IX. Positive (+) sign indicates the presence and the negative (−) the absence of protein zones in the positions designated by letters. Neither their relative intensities of the zones nor their electrophoretic mobilities are considered in this representation.

reasonably claimed at the present level of knowledge is that the qualitative differences in the electropherograms between *Sebastes* and *Sebastodes* are certainly much less in comparison than those between *Scorpaena* and *Sebastolobus*. *Sebastodes aurora* stands uniquely apart from other members of this group and is even suggestive of differences at the generic level if based solely on the criterion of muscle protein patterns.

The muscle protein electropherograms of Fig. 3 are rearranged in Table VIII. Of the four *Sebastodes* groups, 1, 2, and 4 are closely associated, differing among themselves by the presence or absence of only one major zone. Compared with group 4, group 1 lacks protein zone *p*, group 2 possesses the major zone *j* and lacks the minor zone *i*. Group 3 differs from all the other *Sebastodes* in possessing zones *f* and *h* and lacking *a*, *b*, *c*, and *i*.

An intergeneric comparison of muscle proteins of scorpaenids (Table IX) brings out two main features, (*a*) the generic specificity of patterns, and (*b*) the degree of relatedness. *Sebastodes* group 4 is arbitrarily used as the basis

TABLE IX. Intergeneric comparison of muscle proteins of scorpaenids.



Genera	Maximum no. of muscle protein zones																	Comparison with group 4 *Sebastodes*		
	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*	*o*	*p*	*q*	No. of common zones	Type of difference: Addition of zones	Type of difference: Deletion of zones
Sebastodes[a]	+	+	+	−	−	−	−	−	+	−	+	−	+	−	−	+	−	7	0	0
Sebastes	+	+	+	−	−	−	−	−	+	−	+	−	+	−	−	+	+	7	1	0
Scorpaena	−	+	−	+	−	−	−	−	+	−	+	−	+	−	−	+	−	5	1	2
S. aurora[b]	−	−	−	−	−	+	−	+	−	−	+	−	+	−	−	+	−	3	2	4
Scorpaenodes[c]	−	−	−	−	+	−	+	−	+	+	+	−	−	+	+	−	+	2	6	5
Sebastolobus	−	−	−	−	−	−	−	−	+	−	−	+	−	−	+	−	+	1	3	6

[a]Refers to *Sebastodes* group 4.

[b]This species is included in the intergeneric comparison as its muscle protein pattern is so distinctly different from the remaining groups in *Sebastodes*.

[c]The muscle proteins of this species is shown in schematic form only.

of comparison since it includes by far the largest number of species. By this criteria, *Sebastes* possesses one extra major zone *q*, an order of difference similar to groups 1 and 2 of *Sebastodes*. The remaining scorpaenids, in the order of decreasing numbers of common zones, are *Scorpaena*, *S. aurora*, *Scorpaenodes*, and *Sebastolobus*. The details of differences are self-evident in Table IX. *Sebastodes aurora* is included in this intergeneric comparison to point out its position relative to other scorpaenids.

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The authors thank Dr Wilfred Templeman and Mr E. J. Sandeman of the Fisheries Research Board of Canada, Biological Station, St. John's, Nfld., for providing specimens of *Sebastes marinus* and *S. mentella*, and Messrs John E. Fitch and Charles H. Turner, Marine Resources Operations, California State Fisheries Laboratory, for the specimens of *Scorpaena guttata* and *Scorpaenodes xyris*. Messrs D. Davenport and W. R. Harling, of the Nanaimo Biological Station, carried out the age assessments from otolith readings and rendered able assistance at sea in collecting and identifying rockfish specimens. Mr A. P. Ronald, of the Vancouver Laboratory, carried out some of the electrophoretic analyses at sea.

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(APPENDIX TABLE I *follows*)

APPENDIX TABLE I. Location of *G. B Reed* groundfish trawl hauls from which rockfish protein samples were collected, 1965–67.

Haul no.	N lat	W long	Depth (*fath*)
	1965		
65-3-1	51° 25′	129° 00′	100–102
-2	51 23	129 09.5	98–103
-4	51 20	129 05	133–140
-5	51 18	129 18	144–150
-6	51 19.5	129 20	116–122
-7	51 20.5	129 21.5	100–102
-8	51 23	129 24	81–83
-9	57 52	136 53	160–164
-10	57 52	136 50	98–103
-11	57 49.5	136 50	97–106
-13	56 53	136 00	120–140
-15	57 14	136 15	148–180
-16	57 14.6	136 14	114–120
-19	56 49	135 58	122–126
-24	56 19	135 30	104
-26	56 14.5	135 32	142–214
-28	55 42.5	134 45	106–109
-32	55 25.5	134 48.5	117–119
-34	55 30	135 00	112–136
-35	55 16.3	135 07.2	94–100
-37	54 41.5	134 07	122
-38	54 46	134 11	122–200
-39	54 41.5	134 07	122
-40	48 50	126 27	96–98
-43	48 50	126 34	156–160
-48	48 54	126 22.5	84–86
-49	48 55	126 23	86–88
-52	48 32.5	126 06.2	101–104
-55	48 03	125 17.5	86–102
-58	47 07	124 58	108–158
-61	46 39.5	124 44	116–126
-66	46 06.3	124 38.5	97–100
-69	45 29.5	124 26.5	128–134
-74	45 31.5	124 18	90–92
-78	44 25	124 46.5	128–130
-82	43 10	124 42	104–107
	1966		
66-2-1	51 22	128 56	120
-2	51 22.8	128 58	112–120
-4	51 20	129 05	135–140
-9	51 18.5	129 16.5	148–151
-14	54 17	132 31	92–112
-16	54 13	132 42	84–88
-18	54 14	131 57	74–77

(*Continued*)

APPENDIX TABLE I. Location of *G. B. Reed* groundfish trawl hauls from which rockfish protein samples were collected, 1965–67.

Haul no.	N lat	W long	Depth (*fath*)
	1966 (*Con't*)		
66-2-21	54° 42′	134° 05.5′	119–120
-24	54 44.5	134 05.5	117–118
-29	54 06.8	133 25.3	196–200
-30	53 56.5	133 24	37–40
-34	53 22.2	133 07	113
-36	53 19.7	133 02.2	104
-39	52 04.6	130 36.5	120–137
-44	48 21.2	125 51	94–95
-45	48 22.2	125 52.5	94–100
-46	48 23.4	125 53	82–84
-47	49 06.1	126 52.7	122
-48	49 06.6	126 53.6	127–136
-51	49 04.5	126 53.2	178–180
-54	49 11	126 56.4	112–116
-55	49 19.5	127 10.9	122–124
-56	49 22.2	127 22	107–109
-57	50 22.5	128 24.4	104–116
-59	50 23.8	128 23.1	98–111
-61	50 37.1	128 34	94
-62	50 41.4	128 51.6	104–116
-63	50 49.9	129 23	102–104
-64	50 53.3	129 31.4	101–102
	1967		
67-1-1	48 48.5	126 45	194–198
-3	48 58.5	126 45	142–194
-4	49 00	126 44.3	132–152
-10	48 24	126 01	110–112
-12	48 27	125 59	94–96
-13	48 28	126 00	80
-14	48 47	126 22	170–188
-15	48 49	126 20	103–104
-17	48 44.5	126 15.5	100–115
-21	48 47	126 21	150–278
-22	48 47.5	126 27	154–156
-23	48 47.2	126 27	181–188
-24	48 46.7	126 29.5	160–172
-25	48 46.5	126 30	182–202
-27	48 46.5	126 34	222–240
-31	48 47.5	126 20.4	114–124
-34	48 48	126 29.8	159–164
-35	48 47.5	126 31.3	168–176
-37	48 46.4	126 32.2	198–208
-38	48 47	126 34	220–226
-40	48 47.5	126 35.6	286–300

(*Continued*)

APPENDIX TABLE I. Location of *G. B. Reed* groundfish trawl hauls from which rockfish protein samples were collected, 1965–67. — (*Concluded*)

Haul no.	N lat	W long	Depth (*fath*)
	1967 (*Con't*)		
67-1-42	48° 47.8′	126° 33′	180-196
-48	48 54.9	125 12.6	50
-51	48 48.5	126 32.2	150
-53	48 47.5	126 32	192–198
-55	48 47.4	126 34.9	205–214
-68	48 47.5	126 31	205–210
-73	48 48	126 36	298–319
-77	48 20	125 50.5	90
-78	48 24.2	125 52	94–95
-79	48 48	126 33	165–170
-85	48 46	126 31	230–240
-87	50 50.2	129 27.2	101
-90	50 52.5	129 30	102
-92	49 37	127 02	56–60
-93	49 27	127 12.1	97–98
67-2-5	51 14.2	128 38.4	106–110
-9	51 21.4	128 43.5	120
-16	51 11	129 11.4	108–116
-17	51 13.4	129 14.5	152–154
-21	51 16.4	129 27.5	154
-23	51 21	129 21	96–99
-31	55 58.6	135 02.7	200–202
-33	56 02.5	135 05	216–218
-34	56 07.8.	135 24.8	158–166
-36	56 19	135 29.4	115–118
-37	56 17	135 22.3	105–109
-38	56 12.3	136 23.2	120–123
-39	56 10	135 10.5	153–156
-40	56 02	135 05	218–219

NOTES

Abnormal Cessation of Growth in a Herring Otolith

Two remarkably dissimilar otoliths (Fig. 1) have been found in a herring examined during routine sampling at the Fisheries Research Board of Canada, St. John's, Nfld. Biological Station. The fish was one of a sample of 50 herring taken from a purse seine catch made on April 28, 1968 in Baie d'Espoir on the south coast of Newfoundland. It was a ripening female, 305 mm long and weighing 226 g.

There can be no doubt that the two otoliths came from the same fish. Routine sampling procedures at the St. John's Station call for a pair of herring otoliths to be washed and fixed in a depression in a plastic mounting tray as they are removed from the fish (Hourston, 1968). Moreover, the difference in size between the two otoliths was so striking that Mr R. Chaulk, who removed the otoliths, immediately recorded an observation to this effect.

The left (larger) otolith of the pair clearly shows five zones of summer growth (opaque, white areas in Fig. 1). The lack of a winter growth zone (transparent, black area) in the nucleus would indicate that this was a spring-spawned herring of the 1963 year-class. (Summer growth does not show on otoliths from herring in this area until June or July.) Two scales removed from the middorsal area and from behind the pectoral fin respectively also showed 5 full years of growth. The size of the fish was normal for a 5-year-old in this area and its ripening condition suggests that it would have spawned in the late spring, when spawning occurs in this region (Anon., 1967). Thus the left otolith would appear to be entirely normal for a fish of this size taken in this place at this time.

The right (smaller) otolith, on the other hand, shows only two summer growth zones. The dimensions and shapes of these growth zones are virtually identical to those of the first two summer growth zones on the left otolith. The first growth zone is rectangular in shape (more so than for the otoliths from most of the other fish in the sample) and its diameter is about midway between that of the largest and the smallest first growth zones for the other fish in that sample. The second summer growth zone shows a faint check about two-thirds of the way between the first winter zone and the second winter zone (the edge of the right otolith). The outer edge of the second summer zone is fairly irregular along the longer side of both otoliths. The second growth zone on this side of the right otolith is not quite as broad as that in the left otolith suggesting that growth stopped in this area first (before the end of the second summer).

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It would therefore appear that the dimorphism in this pair of otoliths resulted from the right otolith ceasing to develop towards the end of the second summer of growth. A similar situation was observed in cod otoliths by May (1964) except that the smaller otolith was on the right side and had a crystalline development on the postero-dorsal edge. May has since observed this phenomenon several times in cod otoliths (personal communication).

The otoliths in Fig. 1 were photographed by Mr E. L. Rowe in their original mounting and submerged in alcohol.

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(FIG. 1 *opposite*)

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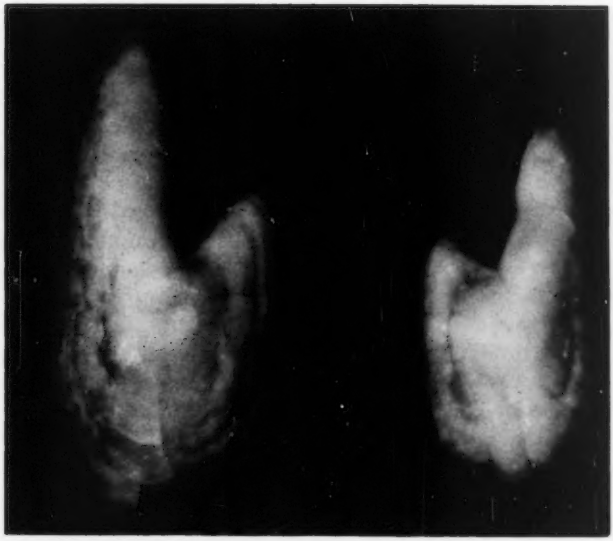

FIG. 1. A pair of herring otoliths (×12) showing five summer growth zones (white) in the left otolith and only two in the right otolith.

Hourston — J. Fish. Res. Bd. Canada

Use of Liquid Scintillation Counting for Measuring Self-Absorption of Carbon-14 in *Daphnia pulex*

This is a report on a liquid scintillation technique for determining a coefficient for self-absorption of radiation. This coefficient includes quenching within animals irradiated.

Self-absorption is defined as absorption of emitted radiation within the sample (Wang and Willis, 1965). The amount is a function of sample thickness and composition. In liquid scintillation counting, this definition requires modification since the fluor may penetrate the sample and be in contact with the emitting substance to a greater or lesser degree. Because of this penetration, self-absorption may be reinforced by quenching within the sample. Quenching in liquid scintillation counting is "any reduction of efficiency in the energy transfer process in the scintillation solution." (Wang and Willis, 1965).

Self-absorption losses in plant and animal tissues are frequently avoided by various combustion techniques which result in bringing the radioisotope into solution in the fluor (Davidson and Oliverio, 1967; Gupta, 1966) in the case of liquid scintillation counting or result in a thin precipitate when the Geiger–Mueller technique is used. A self-absorption curve for the precipitate is then extrapolated to the ordinate to determine counting efficiency at zero precipitate thickness.

Combustion procedures are time consuming and limit the number of samples which can be processed. Sorokin (1966) measured incorporation of ^{14}C in *Daphnia pulex* and other organisms by counting incorporated ^{14}C in whole dried animals and then multiplying these counts by a pre-determined self-absorption coefficient. The self-absorption coefficient was determined from wet combustion of whole labelled organisms and recovery of $^{14}CO_2$ in $Ba^{14}CO_3$ precipitates. The precipitates, on membrane filters, were counted (as were the whole dried animals) with Geiger–Mueller apparatus. Using a self-absorption curve for $Ba^{14}CO_3$ precipitates, Sorokin estimated self-absorption coefficients for *D. pulex* by extrapolating this curve to the ordinate (i.e. to zero thickness precipitate). However, extrapolation of the $Ba^{14}CO_3$ self-absorption curve may lead to errors since the whole curve has not been adequately defined (Jitts and Scott, 1961). Recent applications have indicated that liquid scintillation counting could replace Geiger–Mueller techniques in productivity studies (Wolfe and Schelske, 1967). Self-absorption by the animals can also be measured by liquid scintillation counting. Advantages of scintillation counting are simplicity and precision in calibration, and high counting efficiency with weak beta emitters such as ^{14}C.

In application of the method, animals were exposed to labelled food and then placed in unlabelled media to clear their guts of unincorporated food and wastes. After clearing they were dried for 20 min at 100 C. Ten samples, each

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composed of five animals, were placed in scintillation vials, fluor was added and the emissions were counted. A further 10 samples (five animals each) were combusted in scintillation vials, the products of combustion were dissolved, fluor was added and the emissions were counted. In addition, counting efficiency for the fluor was determined by the channels ratio method so that counts of whole and combusted animals were comparable. The radioactivity standard was carbon-14 hexadecane and the quenching agent was alcoholic picric acid. Samples were counted for 10 min in a Packard Tri-Carb Liquid Scintillation Spectrometer, Model 3003. The fluor used for both whole and combusted animal samples was composed of 50 ml of *p*-dioxane, 80 g of crystallized napthalene, 4 g of PPO, and 100 mg of dimethyl POPOP made up to 1 liter with scintillation grade toluene. The average carbon content of *D. pulex* was 16.4 $\pm$ 1.6 μg C/individual ($n = 330$).

Intact dried animals settled to the bottom of the vials. To determine if the fraction of ^{14}C emissions detected was reduced by settling, three groups of dried, labelled *D. pulex* were each placed in a scintillation vial containing 15 ml of a toluene based fluor (4 g PPO and 100 mg of dimethyl POPOP per liter of scintillation grade toluene). Each group of animals was deposited on a cleared membrane filter supported on a wire stand approximately 12 mm below the surface of the liquid, which had a total depth of 27 mm. The stand was constructed so that the filter was canted at an angle of approximately 10° giving the animals a slight vertical distribution component. Each vial was counted using a Picker Liquimat 220 liquid scintillation counter adjusted to a preset statistic, 1.5% $\pm$ 2σ, which corresponded to 16,400 cpm. After counting, the stand was displaced so that the filter and animals sank to the bottom of the vial. The stand was then placed upright on the filter and the sample recounted. The mean and confidence interval for animals supported off the bottom was 2090 $\pm$ 40.33 dpm; for animals on the bottom of the vials, 2115 $\pm$ 40.54 dpm. It was concluded that settling did not result in a loss of detectable ^{14}C emissions.

The combustion procedure (Gupta, 1966) was as follows: *D. pulex* were placed in small lens-paper cups and dried at 65 C for approximately 25 min. Each paper cup was then placed in a platinum–iridium wire stand in a 25-ml scintillation vial. The vial was flushed for 15 sec with oxygen and then tightly capped. The paper cup and contents were ignited by a beam of light from a 150-w, 120-v Sylvania projection bulb focussed by a simple concavo-convex lens. Immediately after ignition, the vial was immersed in liquid nitrogen contained in a Dewar flask. When bubbling ceased the vial was withdrawn, the cap and platinum wire stand was removed, and 0.1 ml of phenethylamine was added. The cap was replaced and the vial again immersed in liquid nitrogen. After removal from the liquid nitrogen, 10 ml of fluor was added and the radioactivity in the vial measured.

Gupta added phenethylamine prior to combustion; however, this procedure frequently led to partial ignition of the phenethylamine. Consequently it was added after an initial immersion in liquid nitrogen to solidify the products of combustion.

Efficiencies obtained from the quenching curve were used to adjust whole animal counts from cpm to dpm.

Mean activities of intact and combusted animals (Table I) were different ($t = 6.64$, $P < 0.01$) and variances were homogeneous ($F = 2.00$, $P > 0.10$). Self-absorption within *D. pulex* constituted at least 43% of beta emissions. Minor losses may have been associated with the combustion technique. Gupta (1966) estimated that approximately 10% dpm were lost during combustion.

TABLE I. Carbon-14 activity (dpm) of whole and combusted samples of *Daphnia pulex* (five animals per sample).

	Sample										
	1	2	3	4	5	6	7	8	9	10	Mean
Intact animals											
cpm	162.9	213.1	202.5	160.6	165.8	290.5	171.0	175.9	202.1	187.6	
% efficiency	67.8	66.4	66.9	68.0	67.0	65.9	67.8	68.3	65.4	66.4	67.0
dpm	240.3	320.9	302.7	236.2	247.5	440.8	252.2	257.5	309.0	282.5	289.0
Combusted animals											
cpm	367.4	288.9	316.8	404.3	371.3	304.0	236.3	412.3	363.2	272.9	
% efficiency	66.7	66.5	67.2	66.5	67.2	67.5	69.0	66.8	67.4	66.3	67.2
dpm	550.8	428.0	471.4	608.0	552.5	450.4	342.4	617.2	538.9	562.4	512.2

Sorokin (1966) calculated a self-absorption coefficient of 1.66 for *D. pulex* which had carbon contents approximating animals in our experiment (16 μg C/individual). Our average self-absorption coefficient, 1.77 (512/289), was slightly higher. However, the difference may have been due entirely to differences in techniques.

Self-absorption and incorporation of ^{14}C by other small organisms, both terrestrial and aquatic, could be measured using this liquid scintillation technique.

One useful modification of the procedure would be the elimination of the need to freeze by immersion in liquid nitrogen. Instead, phenethylamine could be injected through a serum cap into the vial. The serum cap could subsequently be replaced with a scintillation vial cap.

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First Records of Three Rockfish Species (*Sebastodes aurora*, *S. ciliatus*, and *Sebastolobus altivelis*) from Waters off British Columbia

Off British Columbia, the rockfish family Scorpaenidae is one of the richest in species. Twenty-four species were listed by Clemens and Wilby (1961), and since then six more have been reported (Westrheim, 1964, 1965; McAllister and Westrheim, 1965; Westrheim and Pletcher, 1966; Westrheim and Tsuyuki, 1967).

Three additional species have been noted in the trawl catches of recent *G. B. Reed* groundfish cruises — one during GBR 66-2 and two during GBR 67-1. Station data for these cruises have been reported by Westrheim (MS, 1967) and Harling et al. (MS, 1967), respectively. All specimens were caught in 500-mesh, semi-balloon groundfish trawls.

Aurora rockfish *Sebastodes aurora* (Gilbert 1890)

On March 19, 1967, two rockfish identified as *Sebastodes aurora* (Fig. 1) were collected by the author 30 miles southwest of Amphitrite Point (Vancouver Island) (48°46.8′N lat, 126°35.0′W long) in 230 fath (421 m). One specimen was a female (225 mm standard length) and the other a male (295 mm standard length (SL)). On the same day, and area, two additional specimens (female, 302 mm SL; male, 324 mm SL) were collected in 262–264 fath (479–483 m). On April 13, 1967, in the same area, two specimens (males, 256 and 265 mm SL) were collected in 237–246 fath (433–450 m), and two specimens (males, 273 and 306 mm SL) in 254–266 fath (465–487 m). Water temperatures at depth of capture ranged from 4.8 to 5.6 C and varied inversely with depth.

Sebastodes aurora resembles *S. diploproa* in color and body shape. It can be readily distinguished from *S. diploproa* by the presence of supraocular and nuchal spines, and the absence of the prominent dentigerous knobs on the premaxillaries. Phillips (1957) reports the following distinguishing meristic counts (*S. diploproa* in parentheses): gill rakers, 24–28 (32–37); pores along lateral line, 27–30 (33–43); and diagonal scale rows below the lateral line, 45–50 (53–57).

Meristic counts and morphometric ratios obtained from the eight British Columbia specimens did not differ appreciably from those reported by Phillips (1957) for California specimens.

Phillips (1957) reported the known geographic range as San Diego to Eureka, California; greatest depth taken as 240 fath; and maximum size 13 inches (33 cm), total length. Heyamoto and Hitz (1962) extended the recorded range 400 miles northward to the Oregon–Washington border; the maximum depth to 275 fath (503 m); and maximum size to 36 cm (14.2 inches), fork

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length. The present record extends the recorded range northward approximately 170 miles from the Oregon–Washington border, and the maximum size to 38 cm (15.0 inches), fork length.

The following detailed description of *Sebastodes aurora* follows the format of Clemens and Wilby (1961) and is based on the eight British Columbia specimens. Corresponding morphometric ratios and meristic counts of Phillips (1957) for California specimens are included in parentheses.

Body elongate; depth 2.6–2.9 (2.6–3.2) in standard length. Head with upper profile slightly curved, length 2.4–2.6 (2.4–2.6) in standard length; mouth terminal, moderate; jaws about equal; symphyseal knob small; premaxillaries well separated into two moderate lobes; dentary elevation on lower jaw small; interorbital space at mid-orbits concave, 5.4–6.7 (5.2–6.1) in length of head; cranial ridges well developed; cranial spines: nasal; prefrontal; frontal I, II, III; median frontals, 1, 2, or absent; parietal I, II, sharp, moderately developed; supracleithral and cleithral small; opercular, 2, large; preopercular, 5, pointed, sharp, almost evenly spaced, first and second longest; lacrymal lobes, 2, sharp; rakers on first gill arch, 26–27 (24–28), long, slender. Fins: dorsal (1), XIII, 12–14 (13–14), moderately notched, membranes of spinous portion moderately incised; anal, III, 6 (5–6), second spine stronger than third, equal to or shorter than third; pelvic, 1, 5, thoracic, does not reach anus; pectoral, 17–18 (16–18), 4–8 (0–6) rays unbranched, long, reaching slightly behind origin of anal fin. Scales: ctenoid, large, deciduous; in diagonal rows below the lateral line, 41–48 (45–50). Pores: on lateral line, 28–31 (27–30). Color: rose-red and peach on dorsal surface; silvery on sides and ventral surface; rose-red on lining of mouth and gill cavity; peritoneum, black or silver grey with black dots.

Length to 15 inches.

Distinguished by the small projecting lobes on the upper jaw, and the presence of frontal I and two pair of parietal head spines.

Range: San Diego, California, to Vancouver Island, British Columbia.

The four specimens collected in March have been deposited in the museum of the Institute of Fisheries, University of British Columbia (cat. no. BC 67-12 and 13). The four April specimens have been deposited in the National Museum of Canada (cat. no. NMC 67-728 and 729).

Dusky rockfish *Sebastodes ciliatus* (Tilesius 1810)

On August 30, 1966, a rockfish specimen identified as *Sebastodes ciliatus* (Fig. 2) was collected by W. R. Harling in Dixon Entrance at 84–88 fath (154–161 m) (54°13′N lat, 132°42′W long). The fish was a female, 316 mm (SL). Water temperature at depth of capture was 5.9 C.

Sebastodes ciliatus resembles *S. flavidus*, *S. melanops*, and *S. mystinus*. It differs from *S. flavidus* and *S. melanops* in having a black peritoneum, and from *S. mystinus* by the presence of a prominent symphyseal knob and an anterior (or no) slant to the terminal profile of the anal fin.

Barsukov (1964) reported the known range of *S. ciliatus* as Gulf of Alaska (Portlock Bank to Davidson Bank) and possibly southeastern Bering Sea. Schultz (1936, p. 166) gave the range as Alaska to Neah Bay, Washington. The author examined the three Neah Bay specimens, which were deposited in the United States National Museum (USNM 103726), and found them all to be *S. entomelas*. Specimens of *S. ciliatus* have been noted in the *G. B. Reed* groundfish trawl catches throughout the Gulf of Alaska, from western Alaska (Unalaska Island) to southeastern Alaska (Forrester Island). Numerous specimens from this broad region are on deposit in the National Museum of

Canada (Ottawa) and the museum of the Institute of Fisheries, University of British Columbia (Vancouver). The British Columbia specimen extends the known recorded range southward approximately 800 miles from Portlock Bank.

The following detailed description of the specimen collected in Dixon Entrance is in the format of Clemens and Wilby (1961).

Body elongate, deep, depth 2.6 in standard length; dorsal and ventral profiles evenly curved. Head relatively short, bluntly pointed, length 2.9 in standard length; mouth terminal, large, lower jaw projecting, extending beyond upper profile of head; symphyseal knob prominent; eye diam 4.2 in length of head; interorbital space at mid-orbits convex, broad, 3.9 in length of head; cranial spines: nasal and parietal I, weak; supracleithral and cleithral, short, moderate; opercular, 2, moderate; preopercular short, moderate, third bifid; lacrymal lobes and spines absent; rakers on first gill arch, 35. Fins: dorsal (1), XIII, 15, moderately notched, membranes of spinous portion slightly incised, spines as long as rays; anal, III, 8; pelvic, I, 5, thoracic, not reaching anus; pectoral, 18, 10 rays unbranched, reaching anus. Scales: ctenoid; in diagnoal rows below lateral line, 54. Pores: on lateral line, 48. Color: greenish-brown with brown spots on dorsal surface, paler below; brown streaks radiating posteriorly from eye, 2; dusky to black on all fins; black on peritoneum.

Length to 16 inches.

Distinguished by convex interorbital space, greenish-brown body, prominent symphyseal knob, and black peritoneum.

The British Columbia specimen has been deposited in the museum of the Institute of Fisheries, University of British Columbia (cat. no. BC 66-133).

Longspine channel rockfish · *Sebastolobus altivelis* Gilbert 1893

On April 13, 1967, five rockfish specimens identified as *Sebastolobus altivelis* (Fig. 3) were collected by the author 30 miles southwest of Amphitrite Point (Vancouver Island) in 298–302 fath (545–571 m) (48°46.9′N lat, 126°35′W long). The specimens ranged in size from 113 to 165 mm (SL) — sex was not determined. On the following day, in the same area, an additional five specimens were collected, in 298–319 fath (545–583 m) which ranged in size from 81 to 200 mm (SL) — sex was not determined. Water temperature at depth of capture was 4.8 C.

Phillips (1957) reported the known geographic range of the longspine channel rockfish as Cape San Lucas, Baja California, to Bering Sea, but Clemens and Wilby (1961) did not record this species for British Columbia waters. No specimens were recorded in the rockfish collection of the Institute of Fisheries, University of British Columbia, but six specimens were located in the collection of the National Museum of Canada. Three specimens (NMC 65-324) were collected on August 10, 1965, by D. B. Quayle and associates, aboard the *G. B. Reed*, from an Agassiz trawl catch in 600 fath (1097 m), 14 miles off Marble Island, B.C. (53°01′N lat, 132°55′W long). Standard lengths were 169, 177, and 204 mm — sex was not determined. The remaining three specimens (NMC 66-566) were collected on October 17, 1966, by L. Marhue, aboard the *G. B. Reed*, from a Digby dredge catch made in 300–400 fath (549–732 m) west of the Queen Charlotte Islands (52°31′N lat 131°54′ W long). Standard lengths were 55, 73, and 101 mm — sex was not determined.

All 16 specimens were compared with descriptions listed by Phillips (1957), and no appreciable deviations were noted. *Sebastolobus altivelis* resembles *S. alascanus*, but can be readily distinguished by the dark lining in the gill cover, third dorsal spine (rather than fourth) usually longest, and the second anal fin spine longer and stronger than the third.

The following detailed description of *Sebastolobus altivelis* follows the format of Clemens and Wilby (1961) and is based on the 16 British Columbia specimens. Corresponding morphometric ratios and meristic counts of Phillips (1957) for California specimens are included in parentheses.

Body elongate, slender; depth 3.2–4.5 (3.4–4.1) in standard length. Head with upper profile slightly curved; mouth terminal, large; jaws about equal; symphyseal knob prominent. Cranial ridges and spines numerous, strongly developed; cranial spines: nasal; prefrontal; frontals, I, II, III; parietals, I, II; postorbital series sharp; post-temporal; cleithral; opercular, 2; preopercular, 5, uppermost longest; suborbital ridge sharp, knifelike, spines prominent; lacrymal lobes, 2, sharp spine on each; rakers on first gill arch, 21–25 (21–26), short, stiff, rough, clavate. Fins: dorsal (1), XV–XVI, 8–10 (XV–XVI, 8–10), very deeply notched, membranes of spinous portion deeply incised anteriorly, third, rarely fourth, spine longest, 1.9–3.2 (2.0–3.1) in length of head; anal, III, 5–6 (4–6), second spine longer and stronger than third; pelvic I, 5, thoracic; pectoral, 22–25 (22–24), large, lower portion extended to form distinct lobe of 4–6 exserted rays. Scales ctenoid, large; in oblique rows below lateral line, 32–35 (32–38); present on branchiostegal membranes. Pores on lateral line, 30–32 (28–32). Cirri: nasal, 1, broad. Color: uniform bright red, black markings on fins; black on inner side of operculum and branchiostegal membranes.

Lenght to 15 inches.

Distinguished by: knifelike spinous suborbital ridge; black on inner side of operculum and branchiostegal membranes; third dorsal spine usually longest; and second anal spine longer and stronger than third.

Range: Cape San Lucas, Baja California, to Aleutian Islands, Alaska.

The five specimens collected April 13 were deposited in the museum of the Institute of Fisheries, University of British Columbia (BC 67–11).

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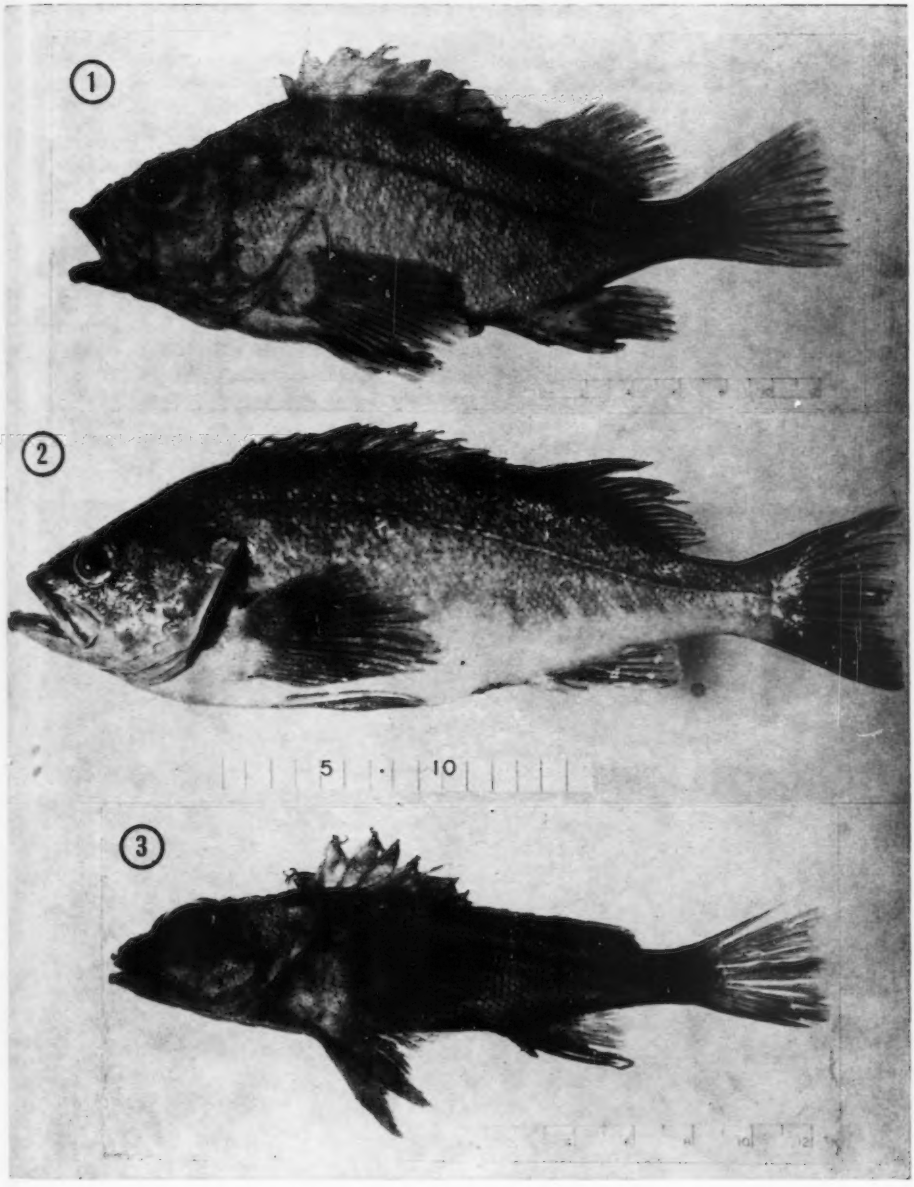

FIG. 1. Aurora rockfish, *Sebastodes aurora*.

FIG. 2. Dusky rockfish, *Sebastodes ciliatus*.

FIG. 3. Longspine channel rockfish, *Sebastolobus altivelis*. (Scale in centimeters for all figures.)

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Calorific Values of Some Invertebrates in Lake Mendota, Wisconsin

Analysis of energy flow through an aquatic ecosystem requires calorific equivalents of its biotic components. Some calorific values have been reported by various workers (Slobodkin and Richman, 1961; Comita and Schindler, 1963; Cummins, MS, 1967), but further measurements are needed to extend our understanding. This report presents calorific values of the dominant invertebrates in Lake Mendota. These analyses have been made during a study of energy transformations in young-of-the-year white bass, *Roccus chrysops* (Rafinesque).

Materials and methods. — The cladocerans were collected with a high-speed tow net (#000 Nitex, 1.024 mm aperture). Amphipods, chironomid larvae, and mayfly nymphs were collected from vegetation (*Myriophyllum* sp.) in the study area. Samples of these organisms were sorted in the laboratory and dried in an oven at 60 C for 24 hr. Dry weights to the nearest 0.1 mg were determined with an analytical balance (Ainsworth SC), and the samples were stored in desiccators. Samples of chitin were obtained by digesting daphnids in a 5% solution of potassium hydroxide. Length measurements of invertebrates were not made before drying because the white bass does not appear to select these organisms according to size. This observation was made during extensive stomach analyses in our laboratory.

Calorific determinations were carried out with a Phillipson microbomb calorimeter (Phillipson, 1964) which measures a temperature rise with a series of thermocouples in contact with the bomb. Changes in temperature were recorded on a potentiometer (Bausch & Lomb VOM 7). The calorimeter was calibrated with benzoic acid of a known calorific content (6318 cal/g). Each sample was pressed into a pellet after grinding and mixing in an agate mortar. Correction was made for heat input to the fuse wire in the bomb, but not for by-products of combustion such as sulfur and acid. An ash fraction for each sample was determined after further combustion for 12 hr in a muffle furnace at 600 C.

Results. — Tables I and II present calorific and ash values for insects and Crustacea over a 3-year period. A mean value of chitin from daphnids is included (Table II) because this material represents a significent portion (15–20%) of the calorific value of each individual and is not digested by the white bass. Moreover, it is a major constituent of the other food species of insects and Crustacea.

For each species there is considerable variation in calorific and ash content between sampling dates (Tables I and II). The low values of the amphipod *Hyalella azteca* seem to be correlated in part with a high ash content. No

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TABLE I. Calorific values of insects. Mean calorific and ash values are given where more than one determination was carried out.

Species	Date collected	Total burned: No. (corrected)[a]	Total burned: Wt (*mg*)	No. of determinations	Cal/g ash-free wt	Range	Ash % dry wt	Range
Glyptotendipes sp. (larvae)	Aug. 17, 1965	16	4.3	1	5752		2.3	
	" 18, 1965	36	10.0	2	5493		3.9	
	" 26, 1966	31	4.9	1	4979		6.1	
	" 14, 1967	73	10.2	1	5321		4.9	
	Nov. 2, 1967	381	10.8	4	5135	4578–5963	6.3	3.2–11.5
Glyptotendipes sp. (pupae)	July 20, 1966	2	1.4	1	5023		0.0	
Caenis sp. (nymphs)	Sept. 27, 1965	10	2.1	1	7130		4.8	
	Aug. 14, 1967	5	1.3	1	6985		0.0	

[a]Unavoidable loss of material during preparation of pellets is corrected in terms of numbers of organisms.

TABLE II. Calorific values of Crustacea. Mean calorific and ash values are given where more than one determination was carried out.

TABLE II. Calorific values of Crustacea. Mean calorific and ash values are given where more than one determination was carried out.

Species	Date collected	Total burned: No. (corrected)[a]	Total burned: Wt (mg)	No. of determinations	Cal/g ash-free wt	Range	Ash % dry wt	Range
Daphnia spp.	Sept. 7, 1965	307	14.2	2	4132		7.6	
	" 8, 1965	305	14.6	2	5364		12.3	
	" 13, 1965	176	8.2	1	4509		13.4	
	Aug. 10, 1966	57	2.9	1	4558		10.3	
	Oct. 17, 1966	155	6.6	1	5643		7.6	
	July 27, 1967	160	8.0	1	4393		10.0	
	Aug. 17, 1967	126	6.9	1	6071		5.5	
	Sept. 16, 1967	273	14.6	4	5381	5068–5820	11.5	2.6–19.5
Daphnia spp. (females with eggs)	Sept. 8, 1965	243	8.6	1	4449		4.6	
	" 11, 1965	126	5.3	1	5652		7.5	
	" 13, 1965	200	7.7	1	4217		6.5	
	" 20, 1965	149	7.8	1	4568		9.0	
	" 27, 1965	68	2.6	1	3776		3.8	
Chitin (from *Daphnia*)	Oct. 28, 1967	1500	10.6	2	5753		12.0	
Leptodora kindti	Sept. 1, 1965	809	29.5	3	5031	4499–5861	7.8	6.5–8.8
	" 13, 1965	462	22.1	2	4652		7.9	
	" 20, 1965	159	7.0	1	5169		10.0	
	Aug. 16, 1966	276	4.7	1	4425		6.4	
	Aug. 26, 1966	226	2.6	1	4724		3.8	
	July 27, 1967	133	12.7	2	4305		10.2	
	Aug. 17, 1967	412	13.0	4	5151	4365–5955	5.5	3.4–6.9
	Sept. 21, 1967	252	16.8	2	4498		1.8	
Hyalella azteca	Aug. 20, 1965	46	6.1	1	3996		8.2	
	Sept. 27, 1965	141	16.6	3	4079	3348–4547	15.7	12.5–17.8
	Aug. 14, 1967	68	12.2	1	3819		22.9	

[a]Unavoidable loss of material during preparation of pellets is corrected in terms of numbers of organisms.

significant differences were observed between samples of mixed daphnids and females with eggs.

Evaluation and significance. — With some exceptions, the calorific values of *Daphnia* spp. and *Leptodora kindti* are comparable with those reported by other authors (Slobodkin and Richman, 1961; Comita and Schindler, 1963; Cummins, MS, 1967). Those for larvae of *Glyptotendipes* sp. are similar to the average calorific equivalents obtained for several species of chironomid larvae by Tubb and Dorris (1965). The absence of significant difference between samples of mixed daphnids and females with eggs suggests the presence of the latter in the mixed samples. Individuals in these samples were not examined during preparation for combustion. The calorific values of the amphipod *H. azteca*, the chironomid larva and pupa *Glyptotendipes* sp., and the mayfly nympth *Caenis* sp. are new additions to the literature. The low calorific content of *H. azteca* may reflect endothermic reactions during combustion, involving decomposition of calcium carbonate in the ash fraction (Paine, 1966).

The results suggest that future research should be focused on the seasonal variation in the calorific content of species and larval instars. Multiple samples of each organism should also be analyzed for each date. This study is presently underway in our laboratory.

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A Rapid Marking Technique for Identification of Individual Fish

Various methods such as finclipping, branding, tatooing, and dyeing have been used to mark large numbers of fish both in the field and in the laboratory (Gerking, 1963; Arnold, 1966; Phinney et al., 1967; Lawler and Fitz-Earle, 1968). We have developed a rapid and efficient technique for marking individual fish with an electrodesiccating instrument (Fig. 1). The instrument,[1] designed for use in human medicine as a cautery unit for electrosurgery, produces very high frequency pulses of electrical energy of low amperage and high voltage. The instrument can be used with several different electrodes. The most satisfactory one for marking fish is the desiccation-fulguration needle. The spark gap oscillator produces a visible spark between the electrode tip and the skin of the fish. The spark is moved along the surface of the fish so as to trace numbers, letters, or other symbols. The heat of the spark desiccates and removes the scales, eventually producing a mark that is dark in color and readily discernible from the surrounding tissue. Histological evidence indicates little damage to the dermal layers of the skin.

The dial of the instrument, which indicates relative voltage outputs, is set at 12.5 or less for fish 3–12 cm long and at 25 for fish 12 cm or more long. The intensity of the output current at these settings is low. Too high a setting may result in damage to the skin or muscle of the fish. The electrode handle is inserted into the white terminal outlet to provide low voltage.

Before marking, each fish is anesthetized with M.S. 222 (tricaine methanesulphonate, Sandoz) in fresh or sea water at room temperature. A concentration of M.S. 222 is used that causes the fish to lose equilibrium in about 1 min. Fish are removed individually from the solution with a dipnet, and placed on a damp paper towel, and excess water is quickly blotted away. Marking is accomplished by bringing the electrode tip close to the skin of the fish with a tapping motion so as to form a series of connected dots. A spark gap of about 0.5 mm is best. Large open letters and numbers such as C, J, Z, X, 7, and 2 should be used as marks rather than closed symbols such as B, D, 6, and 8, since encircling often damages the scale roots. The mark should be made on the side of the fish where it will be most readily visible, e.g., the dorsal side of flatfishes that have a light ventral surface. Marking must be done quickly, and can be accomplished in 5–10 sec. Continual drying of the electrode tip with a paper towel is nessessary to maintain a consistent spark gap. The electrode must not be held near the fish's skin too long because the dermal layers of the skin and musculature can be damaged.

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[1]"Hyfrecator." The Birtcher Corporation, Los Angeles, Calif. Approximate cost $75.00.

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Although the technique was not used in the field, in the laboratory the following fish, some as small as 3 cm long, were marked successfully: 10 striped seaperch (*Embiotoca lateralis*) 5–6 cm long; 80 Lahontan cutthroat trout (*Salmo clarki henshawi*) 6–7 cm long; 160 rainbow trout (*S. gairdneri*) 3–5 cm long; 80 Atlantic salmon (*S. salar*) 3–4 cm long; 420 coho salmon (*Oncorhynchus kisutch*) 3–9 cm long (Fig. 2); 80 chinook salmon (*O. tshawytscha*) 3–5 cm long; and 20 English sole (*Parophrys vetulus*) 7–12 cm long (Fig. 3). Mortality from marking for all fish species was less than 1%. The mark reaches its darkest shade in 1 week; however, it is easily seen immediately after completion. The marks persisted and were visible for 6 months after which time they gradually faded. *Cottus perplexus* could not be marked, presumably because it lacks scales.

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(FIG. 1–3 *follow*)

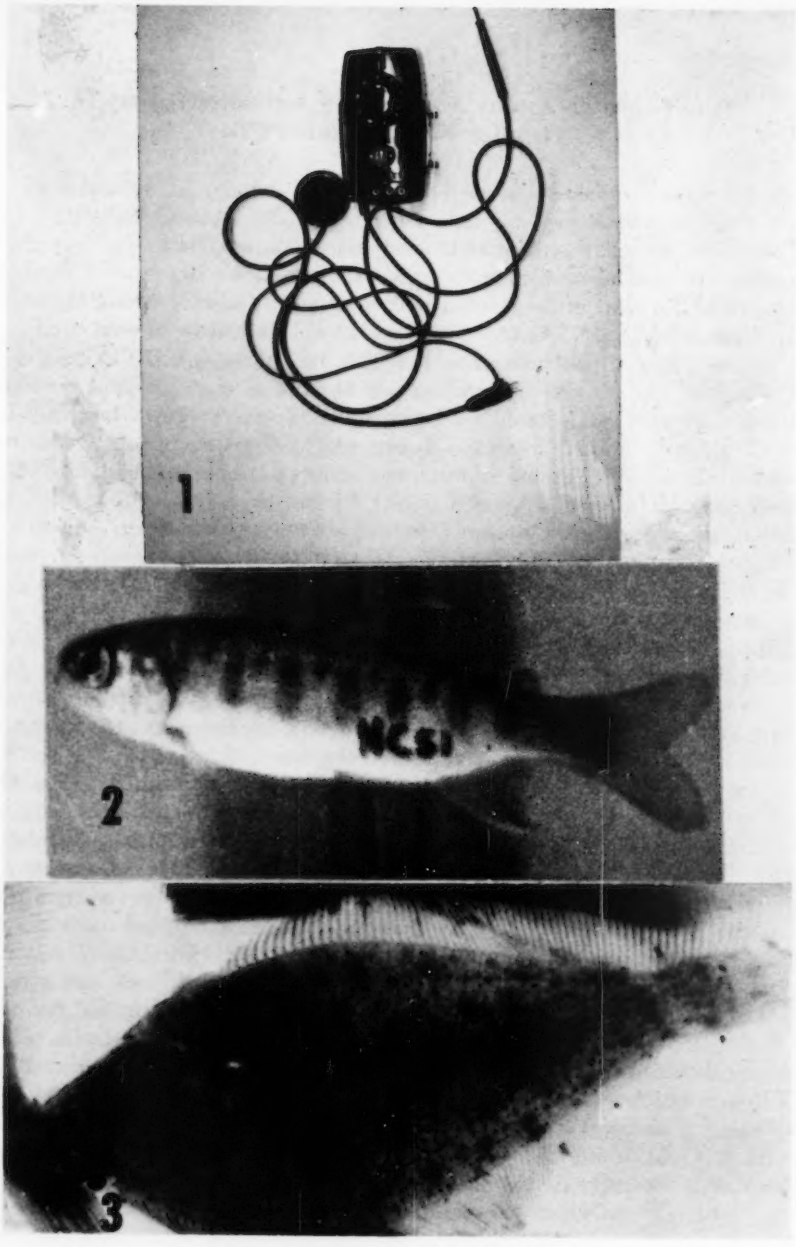

FIG. 1 Electrodesiccating instrument.

FIG. 2. Marked coho salmon.

FIG. 3. Marked English sole.

A Microturbellarian Found in Oysters off the Coast of Prince Edward Island

Examination of oysters, *Crassostrea virginica* (Gmelin), taken off the coast of Prince Edward Island over the past few years, has revealed the presence of large numbers of a small turbellarian. This worm has often been called the "oyster gill worm" because of its close association with the gills of its host. Although it is not possible to describe this worm fully at the present time, it is here identified as belonging to the genus *Urastoma* Dorler, 1900 and is probably *U. cyprinae* (Graff, 1882). This specific identification, however, should remain tentative because of the paucity of fully mature adults.

Urastoma cyprinae was first described by Graff (1882) as *Acmostoma cyprinae*. It was transferred to the genus *Urastoma* Dorler, 1900 by Graff (1903) who indicated that the species described by Dorler (1900) as *U. fausseki* was identical to *U. cyprinae*. Graff (1903) erected a new family, the Genostomatidae, to contain the two genera *Urastoma* Dorler and *Genostoma* Dorler. Reisinger (1924, 1926) transferred Graff's species *cyprinae* from the genus *Urastoma* to the genus *Cylindrostoma* and further indicated that the worm described by Sabussow (1900) as *Enterostoma mytili* was also a synonym of *cyprinae*. Marcus (1951), who discussed fully the classification of both the family Cylindrostomatidae Reisinger and his new family, the Urastomatidae, returned the species *cyprinae* from the genus *Cylindrostoma* back to the genus *Urastoma*. Marcus reasoned that the genera *Cylindrostoma* and *Urastoma* were quite different using the classification proposed by Karling (1940). Marcus (1951) also described a new species, *Urastoma evelinae*, which he separated from *U. cyprinae* on six points. These differences, however, do not appear to be major and Westblad (1955) indicated that *U. evelinae* also may be synonomous with *U. cyprinae*.

Urastoma cyprinae was first found in the mantle cavity of *Cyprina islandica* and has since been recorded from *Mytilus edulis*, *Solen vagina*, and *Modiola modiolus*. Westblad (1955) found large numbers of *U. cyprinae* free-living in red algae near Rovinj Station, Yugoslavia, and Marcus (1951) previously described his species, *U. evelinae*, also as free-living among the littoral algae off the island of São Sebastião, Brazil.

Urastoma cyprinae was considered initially to be a parasite of lamellibranch molluscs. Its occurrence as a free-living organism, however, indicates no obligatory relationship with a host and suggests that *U. cyprinae* is probably a facultative commensal associated with various lamellibranchs.

The present findings represent the first report of *U. cyprinae* from North America and also the first record from *Crassostrea virginica*.

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Triaenophorus nodulosus in Burbot, *Lota lota*, from Heming Lake, Manitoba

Members of the genus *Triaenophorus* are widely distributed in temperate zone fish up to the northern limits in which pike, *Esox lucius*, are found. The pike serves as the definitive host of *Triaenophorus nodulosus* (Pallas, 1781), and several species of fish including the yellow perch, *Perca flavescens*, and the burbot, *Lota lota*, act as second intermediate hosts. The second intermediate stage consists of plerocercoids enclosed in fibrous cysts which are found in the body cavities of fish, especially in the liver. According to Bauer (1959) the plerocercoids are considered pathogenic, causing degeneration of internal organs, especially the liver, and may cause the mass death of fish. He cited one case of a burbot liver from the northern part of Lake Onega in which the tissue was almost completely destroyed and only the membrane containing many cysts remained. In another report from the USSR, Volkova (1941) noted that mass infection of burbot livers from the lower reaches of the Ob River necessitated the rejection of this valuable product for canning.

Burbot have never been really abundant in Heming Lake; their numbers increased during the late 1950's with increased fishing pressure, although not nearly as much as other species. Adult burbot are found most frequently in deeper, cooler waters but young burbot are often found inshore in rocky areas during the summer. They are not readily taken in seines because of the difficulties in manipulating the gear in this habitat but can best be captured by scattering fish poison over the area and catching the fish with a dipnet when they rise. Burbot have a tendency to burrow when the poison begins to take effect but the young-of-the-year and juvenile burbot are readily visible on the bottom as the ventral part of their body is milky white, in contrast to the darker lake bottom.

Shore poisoning with 5% emulsifiable rotenone during late June, July, and August in a few rocky areas during the early 1950's showed that there was a substantial population of young burbot but, as stated earlier, these numbers were not reflected in the catch of adult fish. Samples of these young fish were autopsied and the presence of *T. nodulosus* was noted. This was not unexpected as Miller (1945) had previously recorded the presence of this parasite in burbot in Canada. However, the data obtained from Heming Lake burbot are more quantitative.

Sixty-six burbot ranging from 100 to 547 mm total length were examined. The majority of the fish were less than 180 mm long. The incidence of infection in the sample is shown in Table I. Over 80% of the fish contained *T. nodulosus* and 76% of all infected fish had more than one cyst per fish. Although the sample size is small the data in Table I do show that the smaller fish are more heavily infected than are the larger fish. Most of the cysts were

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TABLE I. Incidence of *Triaenophorus nodulosus* in Heming Lake burbot.

Size-range (*mm*)	No. of cysts							
	0	1	2	3	4	5	6	7
100–119		2	1	1	1			1
120–139	2	5	6	5	2	1	2	1
140–159	2	2	5	1	6	3		
160–179	3	2	1	2	1			
180–199	1				1			
200–219	1							
220–239	1							
240–259				1				
260–279	1							
280–299								
300–319		1						
Z								
547		1						
Totals:	11	13	13	10	11	4	2	2

found in the liver but some were attached to the intestine and to the stomach. One fish (113 mm) had practically more cysts than liver and in another fish (138 mm) no liver tissue was visible. Such evidence seems to agree with the findings of the European investigations previously cited and it is highly possible that *T. nodulosus*, particularly as it affects the very young burbot, may be important in influencing the success of year-classes after hatching. At Heming Lake, the burbot spawn about early March and hatching occurs approximately 1.5–2.5 months later. The young-of-the-year would likely still be feeding on plankton when the parasite is in its early stage in a copepod host ready to be consumed by the next host in the life cycle, in this instance, the burbot.

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